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SEASONAL CHANGES IN THE CHEMICAL COMPOSITION OF APPLE SPURS

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SEASONAL CHANGES IN THE CHEMICAL COMPOSITION OF APPLE SPURS

H. D. HOOKER, JR.

SUMMARY

Samples of apple spurs with leaves, flowers or fruit removed were collected at intervals during a year and their chemical composition studied in relation to their physiological condition.

Three types were investigated: spurs that blossomed and bore fruit; spurs that did not blossom, but which developed fruit-buds; and barren spurs that neither blossomed nor developed fruit-buds. The first type is represented by samples from Wealthy, Ben Davis and Jonathan trees; the second by samples from Jonathan and Ben Davis trees—the Jonathan being the same one from which samples of the first type were taken; the third by samples from Ben Davis and Nixonite trees.

Determinations were made of the dry weight, ash, titratable acidity, potassium, phosphorus, total nitrogen, reducing and non-reducing sugars, starch, total polysaccharides and hydrogen ion concentration. In general, official analytical methods of the A. O. A. C. were used. The starch values were obtained by digestion, followed by hydrolysis of the digestion products. Some supplementary microchemical tests were made.

1. The seasonal changes in most of the constituents examined are distinct and characteristic of the condition of the spur, bearing, non-bearing, or barren. In general the bearing and sterile spurs show extreme values, while the non-bearing spurs assume a position intermediate between them.

2. The conditions characteristic of bearing and non-bearing spurs of the same tree (Jonathan) are practically identical with the conditions of spurs from different trees (Ben Davis) in bearing and in the off year respectively. Spurs from barren trees are char-

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acterized by a seasonal chemical picture distinctly different from the two types of spurs from productive trees.

3. For most constituents, the spurs pass thru one period of maximum content and one of minimum content during the course of the year. In the cases of starch and titratable acidity there are two maxima and two minima, the maxima of one coming at approximately the same time as the minima of the other. Carbohydrate consumption and acidity seem to be correlated.

4. Conditions leading to high starch and low nitrogen content at the time of fruit-bud differentiation appear to be essential for productivity. Fruit-bearing spurs that develop leaf buds have a low starch and high nitrogen content, and barren spurs have a low starch and low nitrogen content. The starch-nitrogen ratio is more indicative than the total carbohydrate-nitrogen ratio.

5. During the late summer and fall there is a steady increase in the phosphorus and nitrogen content of spurs with fruit buds. The absence of this feature in barren spurs suggests a necessity for phosphorus and nitrogen storage, making possible the marked increase in these elements that is peculiar to bearing spurs in the spring.

INTRODUCTION

An organism reacts to changes in its relations with the environment by means of definite responses. These responses produce changes in morphological structure which are manifestations of alterations in the chemical equilibrium of the organism. This means that there is a correspondence between the chemical composition of an organism and its physiological behavior.¹ Numerous attempts have been made to show the existence and nature of this correspondence, that is, to show the differences in chemical composition that accompany changes in morphological structure.

More particular attention has been devoted to the chemical changes in plants which accompany a transition from the vegetative to the reproductive condition and some degree of correlation has been found between the condition of fruitfulness and the ratio of the carbohydrate to the nitrogen content. Fischer² found that

1. Altho these principles are well known, the conception that structure and chemical composition are different aspects of the same thing has not entirely displaced the idea that one is the cause or effect of the other. Cf. Hooker, H. D., Jr. Behavior and Assimilation. Am. Nat. 53: 509, 1919.

2. Fisher, H. Zur Frage der Kolensäure-Ernährung der Pflanze. Gartenflora 65: 232-237. 1916.

the vegetative condition was characterized by a carbohydrate content relatively low in proportion to the nitrogen content or in other words by a low carbohydrate-nitrogen ratio. He found that the reproductive condition was characterized by a carbohydrate content relatively high in proportion to the nitrogen content or in other words by a high carbohydrate-nitrogen ratio.

Kraus and Kraybill³ have confirmed these findings by their work on "Vegetation and Reproduction with special reference to the Tomato," but they find in addition to the two categories recognized by Fischer, two other categories. The four types which these authors distinguish are:

1. A very high carbohydrate-nitrogen ratio accompanying a weakly vegetative condition. In this type nitrogen appears to be a limiting factor of growth and the high ratio is apparently due to the small amount of nitrogen present. It seems probable that the amount of available carbohydrate is an indifferent factor and that the nitrogen content is the determining constituent.

2. A high carbohydrate-nitrogen ratio accompanying abundant fruit production. In this type nitrogen compounds are available, but the high ratio is due to an excess of carbohydrates. This is one of the types recognized by Fischer.

3. A low carbohydrate-nitrogen ratio accompanying a vigorous vegetative condition. In this type there appears to be an available supply of both carbohydrate and nitrogen and the balance between them is such as to produce the best vegetative conditions without leaving a residue of carbohydrate. This is the other type recognized by Fischer.

4. An exceedingly low carbohydrate-nitrogen ratio accompanying a weakly vegetative condition. In this type carbohydrate appears to be the limiting factor of growth and the low ratio is due to the small amount of carbohydrate present. Here the amount of available nitrogen appears to be an indifferent factor.

These valuable contributions mark a new trend of investigation in the field. Attention has been confined, however, to a limited number of constituents—moisture, carbohydrates and nitrogenous compounds. For a more thoro knowledge of the alterations in the chemical equilibrium of the plant and their correspondence to changes in morphological structure a wider range of constituents must be investigated. In the present investigation therefore, in addition to determinations of moisture, total nitrogen, reducing and

3. Kraus, E. J. and Kraybill, H. R. Oregon Agr. Exp. Sta. Bul. 149, 1918.

non-reducing sugars, starch and total polysaccharides, further determinations were made of the titratable acidity, hydrogen ion concentration, total ash, potassium and phosphorus.

Numerous analyses of these constituents in various plant tissues, including the apple, have been made⁴ but their value is seriously impaired because the material analyzed has, except in a few instances, been collected at only one season of the year, usually in the fall. However, Richter⁵ has studied the nitrogen and ash content of leaves at different ages; Truelle⁶ has investigated the variations in some constituents of the developing fruit; and Butler, Smith, and Curry⁷ have recently made a detailed study of the distribution of food materials in the shoots, trunk, and roots of apple trees at different periods of vegetation. In order to bring out correspondences between chemical composition and physiological behavior, it is necessary to have analyses on comparable samples collected at intervals thruout the year. Differences in chemical composition which correspond to different physiological conditions may be in evidence at one season of the year, that is, at one stage in the seasonal development of the plant, such as the period of fruit-bud differentiation, while at other seasons or stages no such differences may exist. Successive analyses of the sort indicated were made by Kraus and Kraybill on the tomato and have been made by other investigators on various annual plants.⁸ But practically the only available data concerning the seasonal variations in the chemical composition of trees beside those already mentioned are the analyses of the carbohydrate, nitrogen, ether extract and moisture content of various trees, including the pear and chestnut, made by Leclerc du Sablon.⁹

The collection of data showing seasonal variations in the chem-

4. Cf. Thompson, R. C. The relation of fruit growing to soil fertility. *Ark. Agr. Exp. Sta. Bul.* 123. 1916.

5. Richter, L. Mineralstoffgehalt der Obstbaumblätter in verschiedenen Wachstumszeiten. *Landw. Versuchs-Sta.* 73: 457-477. 1910.

6. Truelle, A. Étude d'une variété de pomme à cidre à tous les ages. *Comptes Rendus* 117: 765-767. 1893.

7. Butler, O. R., Smith, T. O. and Curry, B. E. Physiology of the apple. Distribution of food materials in the tree at different periods of vegetation. *N. H. Agr. Exp. Sta. Tech. Bul.* 13. 1917.

8. Jones, W. J., Jr. and Huston, H. A. Composition of maize at various stages of growth. *Ind. Agr. Exp. Sta. Bul.* 175. 1914. Willaman, J. J., West, R. M., Sprietsterbach, D. O. and Hohn, G. E. Notes on the composition of the sorghum plant. *Jour. Agr. Research.* 18: 1-31. 1919. Burd, J. S. Rate of absorption of soil constituents at successive stages of plant growth. *Jour. Agr. Research.* 18: 51-72. 1919.

9. Leclerc du Sablon. Recherches physiologiques sur les matières de réserve des arbres. *Rev. gén. bot.* 16: 341-368; 386-401. 1904. *ibid.* 18: 5-25; 82-96. 1906.

ical composition of fruit trees and their correlation with physiological condition has a distinctly practical value. When such correlations have been well established, it will be possible to describe the normal chemical composition corresponding to a definite physiological state and the degree of variation which may be expected from this norm. Moreover a thoro knowledge of these correlations will show what constituents are indicative and should be determined in the study of any particular physiological condition, such as the condition of fruitfulness. The work of Fischer, Kraus and Kraybill shows that ratios between constituents may be just as indicative, if not more so, than their absolute amounts. With this knowledge as a basis it will be possible to diagnose the condition of any particular tree or orchard and the diagnosis will indicate the direction in which changes should be effected. Diagnosis is the key to scientific orchard management.¹⁰

COLLECTION OF MATERIAL

In an attempt to find some convenient means for ascertaining the actually prevailing conditions in bearing and non-bearing apple trees, samples of the fruit spurs were collected for analysis. This portion of the plant was selected as being probably most indicative of differences in the normal behavior of bearing and non-bearing trees.

Three types of samples were collected: spurs that blossomed and bore fruit; spurs that did not blossom, but which gave promise of developing fruit buds during the season of collection; and barren spurs that did not blossom and developed only leaf buds. The first type which may be termed fertile or bearing spurs were collected from trees of three varieties.

1. A Wealthy tree with a tendency toward alternate bearing. The year the samples were taken the tree bore a heavy crop of fruit.

2. A Ben Davis tree likewise with a strong tendency toward alternate bearing. The year the samples were taken this tree also bore a heavy crop of fruit.

3. A Jonathan tree which is a constant and heavy bearer.

The second type which may be termed non-bearing spurs were for the most part spurs that had borne the previous season and a considerable percentage of which were developing fruit buds the

10. Cf. Hooker, H. D., Jr. Methods of approach to horticultural problems. Proc. Am. Soc. Hort. Sci. 16: 140-145. 1919.

year the samples were taken. They were collected from trees of two varieties.

1. A Jonathan tree, the same tree from which the last mentioned samples were collected. These represent spurs in the off year on a tree in full bearing.

2. A Ben Davis tree with the alternate bearing habit which bore heavily the previous season but had a very small crop the year the samples were taken.

The third type which may be termed barren spurs were taken from trees that had never borne a full crop of fruit. These spurs were collected from trees of two varieties.

1. A Ben Davis tree, which is apparently sub-normal. It is of the same age as the other trees and tho smaller, might yield about six bushels of apples a year. In spite of this it produces ten or a dozen apples.

2. A Nixonite tree, which grows luxuriantly and from which a dozen bushels of apples might be expected. Instead it bears perhaps a dozen apples a year.

All of these trees are growing on the grounds of the Horticultural Department in Columbia, Mo. The Wealthy and Nixonite trees are growing close to each other in one part of the orchard and the three Ben Davis trees and the Jonathan tree are growing near one another in another part of the orchard. All of these trees are grown under sod and are approximately twenty years old. They are all in good condition and have received careful treatment as regards pruning and spraying.

The samples analyzed were collected at six different times of the year. The first samples were taken in the spring of 1919 before the buds broke. The season was early and the swelling of the buds facilitated the discrimination of leaf and fruit buds. The samples of non-bearing spurs were made on the assumption that spurs which had borne fruit the previous year would not bear this year. The samples of the Wealthy and the Nixonite were collected February 4. The samples of bearing and non-bearing spurs from the Jonathan tree were collected March 11. The samples from the three Ben Davis trees were collected March 26. These samples included one year's growth except in the case of the spurs of the Nixonite and the barren Ben Davis trees. A year's growth on their spurs was so short that the entire spur was taken for analysis. This was done advisedly to make these samples more comparable with those of the bearing and non-bearing spurs, as it was thought

that on account of this small yearly increment older tissue influenced development and growth. There was no danger of confusing spurs that are here classed as non-bearing with those classed as barren. The first group was of vigorous non-producing spurs from productive trees. The second group was of equally vigorous spurs but from trees known to be unproductive and with little promise of bearing in the near future.

The second collection of samples in this series was made May 13. At this time blossoming was about over. The leaves and blossoms were removed from the bearing spurs, and the leaves were removed from the non-bearing and barren spurs. The samples included last year's wood together with the new growth except in the case of the barren spurs where the entire spur was used for analysis.

The third collection of samples was made June 26, approximately in the middle of the period of fruit bud differentiation. Leaves and apples were removed from the bearing spurs and leaves from the non-bearing and barren spurs. In this and the previous collection there was, of course, no difficulty in distinguishing bearing from non-bearing spurs.

The fourth collection of samples was made September 2. Leaves and fruit were removed from the bearing spurs of the Jonathan and the Ben Davis. The apples had already been picked from the Wealthy tree. Spurs which showed evidence of having borne fruit were collected from this tree and the leaves were removed from them and from the non-bearing and barren spurs.

The fifth collection of samples was made November 19 when practically all of the leaves had fallen from the tree. Any that remained were removed from the material collected. The fruit of the Jonathan and Ben Davis trees had been picked approximately five weeks previous to the collection of the samples.

The last collection of samples in this series was made January 24, 1920. Spurs of the first type now showed scars where fruit had been borne and had leaf buds. Spurs of the second type had fruit buds, thus reversing the position of these two types from their position at the time the first samples were taken.

The size of sample collected was limited by two considerations; first, that sufficient material be left for subsequent sampling, and second, that the amount of material removed should not be so great as to constitute a severe pruning and so alter the physiological and chemical condition of the tree and hence of the

spurs that remained for subsequent sampling. Each sample consisted of from forty to seventy spurs and the fresh weight was usually between twenty-five and thirty grams. This was about the minimum on which the number of analyses planned could be carried out.

For the sake of uniformity all samples were collected between nine and eleven o'clock in the morning following a clear dry day.

METHODS OF ANALYSIS

As wide a range of constituents were determined as the size of the samples permitted. The determinations made included dry weight, ash, potassium, phosphorus, total nitrogen, reducing sugars, total sugars, starch, total polysaccharides, titratable acidity, and hydrogen ion concentration. Nitrate determinations were made both analytically and microchemically but no evidence of their presence in spurs at the times when collections were made was obtained. Determinations of calcium, sulphur and amino nitrogen were contemplated and would have been advisable but the size of the samples did not permit the inclusion of these analyses. The ash, potassium, phosphorus and total nitrogen determinations were made by the Department of Agricultural Chemistry of the Experiment Station.

Dry Weight.—As soon as the spurs were cut from the tree they were placed in weighed bottles and tightly corked. These were taken to the laboratory and weighed immediately. The bottles were then placed in a constant temperature oven and the sample was dried at 75° C. Samples were dried to constant weight in from sixty to seventy-two hours. The bottles were then recorked, allowed to cool, weighed, and the dry weight obtained by difference.

Ash.—The dried material was pulverized in a mill. One gram samples of the powder were used for ash determinations. In order to conserve material the ash analysis was run in conjunction with either the potassium or phosphorus analyses.

Potassium.—One gram of the dry powder was ashed, leached with hot water and the residue with the filter paper was burned. A J. Lawrence Smith fusion was run on this residue. It was then leached and the filtrate was combined with the leachings from the first ash. Potassium was determined by the official Lindo-Gladding method on the combined solutions.

Phosphorus.—One or two grams of the dry powder were

ashed, digested with hydrochloric acid, nitric acid was added and the hydrochloric evaporated off. The official gravimetric method was used on the nitric-acid solution.

Total Nitrogen—One gram of the dry powder was used for the determination of total nitrogen. The official Kjehldahl-Gunning-Arnold method was used.

Carbohydrates.—1. *Reducing Sugars.* One or two grams of the dry powder were thrown on a filter and washed at least five times with small amounts of cold distilled water into a 250 cc. volumetric flask. The washings were used for the determination of sugars; the residue was saved for starch analysis. The solution was cleared with basic lead acetate solution until no further precipitate developed on the addition of a drop of the reagent. The extract was then made up to volume, thoroly mixed and filtered thru a dry folded filter paper. Two hundred cubic centimeters of the filtrate were transferred to a 250 cc. volumetric flask, and sufficient dry sodium carbonate was added to precipitate any excess of lead. The solution was made up to volume, thoroly mixed and filtered thru double folded filter papers into a dry flask. The filtrate was used for the determination of reducing sugars.

2. *Total Sugars.* Seventy-five cubic centimeters of the last filtrate were pipetted into a 100 cc. volumetric flask graduated to deliver. Five cubic centimeters of concentrated hydrochloric acid (sp. gr. 1.19) were added slowly and the contents were thoroly mixed. The flask was then placed in a constant temperature water bath at 70° C. for ten minutes to hydrolize compound sugars. The flask was allowed to cool and the contents were made neutral to litmus paper and after cooling made up to volume. The clear solution was used for the determination of total sugars as glucose.

3. *Starch.* The sugar-free residue from the washings of the powdered sample was used for the determinations of starch. The filter paper was punctured and the residue washed into a small beaker. The contents were boiled for five minutes in order to convert all the starch present into a paste. The beaker was covered with a watch glass. After cooling, 3 cc. of a concentrated solution of Taka-diastase were added. The material was then incubated at 50° C. for twenty-four hours to convert the starch to maltose and dextrin. It was then thrown on a filter paper and the products of digestion were washed into a 700 cc. pyrex flask. Eight cubic centimeters of concentrated hydrochloric acid (sp. gr. 1.19) were mixed with enough cold water to bring the total volume of the filtrate up to 150 cc. and were added to the flask. The flask was connected to a reflux condensor and the con-

tents boiled for two hours and a half to hydrolyze maltose and dextrin to glucose. After cooling, the solution was neutralized with sodium hydroxide and transferred to a 250 cc. volumetric flask with washings. The solution was then cleared with basic lead acetate solution, made up to volume, mixed and filtered. Two hundred cubic centimeters of the filtrate were transferred to a 250 cc. volumetric flask. The excess lead was precipitated with solid sodium carbonate. The solution was then made up to volume, mixed and filtered thru double folded filter papers. The filtrate was used for the determination of starch as glucose. With each lot of starch determinations a blank was run on 3 cc. of the Taka-diastase solution. The reducing power of this solution was determined and subtracted from the reducing power of the digested and hydrolyzed starch preparation. The difference gives the amount of starch as glucose.

4. *Total Polysaccharides.* One-half gram of the dry powdered material was washed at least five times with small quantities of cold distilled water. The washings were used for the titration of acidity. The filter paper was punctured and the residue washed into a 700 cc. pyrex flask. Eight cubic centimeters of concentrated hydrochloric acid (sp. gr. 1.19) were mixed with enough water to bring the total volume of the washings to 150 cc. and were added. The flask was connected to a reflux condenser and the contents boiled for two and a half hours. After cooling, the red solution was neutralized with sodium hydroxide using the natural indicator present to determine the end point. Neutrality is reached when the red color of the solution first begins to change to dark green. The neutralized material was transferred to a 250 cc. volumetric flask with washings. The solution was cleared with basic lead acetate solution, made up to volume, mixed and filtered. Two hundred cubic centimeters of the filtrate were pipetted into a 250 cc. volumetric flask, the excess lead was precipitated with solid sodium carbonate; the solution was made up to volume, mixed and filtered thru double folded filter papers. The clear filtrate was used for the determination of total polysaccharides as glucose.

The reducing power of these sugar solutions was determined by the official Munson-Walker method. Fifty cubic centimeters of each solution was used. The reduced copper was collected in a tared Gooch crucible, burned and weighed as black copper oxide. It was eventually found more convenient to collect the reduced copper on an ashless filter paper, burn and weigh.

Titratable Acidity.—The washings of the half gram sample used in the determination of total polysaccharides was titrated to

neutrality with n/10 sodium hydroxide using neutral red as an indicator. The end point was determined by matching the color against a standard solution of phosphates containing the same amount of indicator and having the same volume as the solution titrated. This standard had a pH value of 7.4 and was made by mixing four parts of m/15 dibasic sodium phosphate ($\text{Na}_2\text{HPO}_4 \cdot 2\text{H}_2\text{O}$) with one part of m/15 mono-basic potassium phosphate (KH_2PO_4). In case the extract used for titration was highly colored, and this was usually the case, a flask containing a sample of the same volume and concentration as that titrated was placed behind the standard and a flask containing water behind the solution titrated. The end point was reached when by looking thru the flasks arranged as indicated, the colors matched.

Hydrogen Ion Concentration.—The indicator method was used. Water and the indicator were added to a test tube with washings of a small quantity of the dry powder. A test tube containing water was placed behind this and a test tube containing some of the washings behind the standard. The hydrogen ion concentration was determined by matching the colors of the plant extract with the standards.

The standards for pH 7.0, 6.7, 6.4 and 6.0 were made up from solutions of m/15 disodium hydrogen phosphate ($\text{Na}_2\text{HPO}_4 \cdot 2\text{H}_2\text{O}$) and of m/15 mono-potassium dihydrogen phosphate KH_2PO_4 , as follows:

pH 7.0—30.5 parts of dibasic to 19.5 parts of mono-basic phosphate solution.

pH 6.7—43.0 parts of dibasic to 57.0 parts of mono-basic phosphate solution.

pH 6.4—26.0 parts of dibasic to 74.0 parts of mono-basic phosphate solution.

pH 6.0—12.0 parts of dibasic to 88.0 parts of mono-basic phosphate solution.

The standards for pH 6.0, 5.7, 5.3 and 4.9 were made from n/10 acetic acid and n/10 sodium hydroxide as follows.

pH 6.0—24.15 cc. n/10 acetic acid and 23 cc. n/10 NaOH diluted to 250 cc.

pH 5.7—25.30 cc. n/10 acetic acid and 23 cc. n/10 NaOH diluted to 250 cc.

pH 5.3—28.75 cc. n/10 acetic acid and 23 cc. n/10 NaOH diluted to 250 cc.

pH 4.9—34.50 cc. n/10 acetic acid and 23 cc. n/10 NaOH diluted to 250 cc.

Alizarine sodium sulphonate was used as the indicator for pH, 7.0, 6.7, 6.0, 5.7, 5.3 and 4.9. These determinations were checked with neutral red as an indicator for pH 7.0, 6.7, 6.4, and 6.0 and methyl red as an indicator for pH 6.4, 5.7, 5.3 and 4.9.

PRESENTATION OF DATA

The results of analyses of the material described are given in Tables 1 to 25. All determinations were run in duplicate and each number represents the average of two analyses that check. The fresh weight figures are calculated from the percentages of dry weight. These data are represented graphically in Figures 1 to 24. In these figures the values for the bearing spurs are represented by continuous lines marked W, B and J for Wealthy, Ben Davis, and Jonathan, respectively. The values for the non-bearing spurs are shown by broken lines marked J and B for Jonathan and Ben Davis, respectively. The values for the barren spurs are given by dotted lines marked B and N for Ben Davis and Nixonite, respectively. Each figure shows the variations in the period of one year beginning February 1, 1919 and ending January 31, 1920.

The percentages of dry weight are given in Table 1 and in Figure 1. The curves show minima in May for all three classes of spurs. The greatest drop occurs in the bearing spurs, the least in

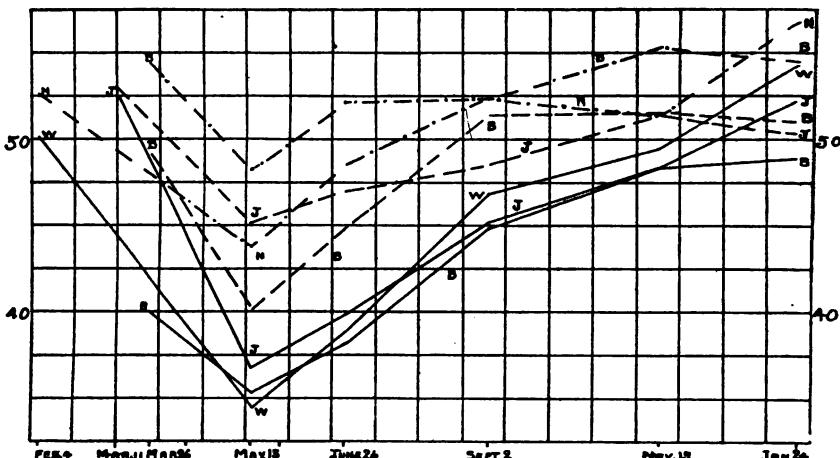


FIG. 1.—Graphs showing variation in percentages of dry weight. The notation is described in the text

the barren spurs, while the non-bearing spurs are intermediate. The maxima for the dry-weight curves of the bearing spurs occur in January, for the non-bearing spurs in November and for the barren spurs probably at sometime between these two dates. During the winter the spurs with flower buds have lower percentages of dry weight than those with leaf buds. Thruout their course the percentages of dry weight for the barren spurs are high, for the bearing spurs relatively low while the non-bearing spurs are intermediate. The bearing and non-bearing spurs of this season are the non-bearing and bearing spurs respectively of the coming season and consequently the curves exchange places. In this case this occurs during the winter. The greatest difference between the various types occur in May or June.

The percentages of ash in terms of dry weight are given in Table 2 and the curves are shown in Figure 2. In the spring the

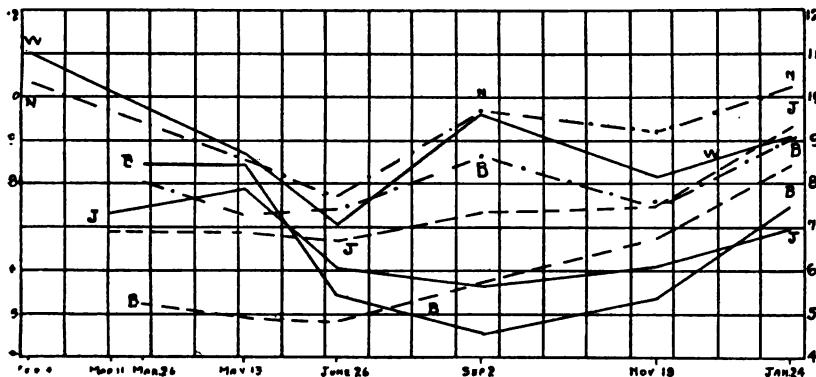


FIG. 2.—Graphs showing variation of ash in percentages of dry weight

bearing and barren spurs have a higher ash content than the non-bearing spurs, but during May and June the ash content of the bearing spurs decreases rapidly. The Jonathan and Ben Davis spurs continue to lose ash until September when the curve reaches its minimum. The Wealthy spurs increase in ash content after June and reach a maximum in September, then decrease until November and increase during the winter at which time all of the spurs have a high ash content. The non-bearing spurs have a fairly constant ash content thruout the growing season with the lowest values in June, after this the ash content rises steadily to a maximum in January. The bearing and non-bearing spurs exchange positions in June or July so that at the end of the year the

spurs which will bear fruit have a higher ash content than those which have borne fruit during the year and will produce leaves the coming season. The barren spurs have a relatively high ash content thruout the year, showing slight fluctuations.

The percentages of ash on the fresh-weight basis are given in Table 3 and the curves are shown in Figure 3. In general, the picture is the same as that in Figure 2.

The values for titratable acidity in terms of dry weight are given in Table 4 and their graphical representation is given in Figure 4. The curves are characterized by two maxima and two minima; the maxima for the bearing spurs occur in June and Jan-

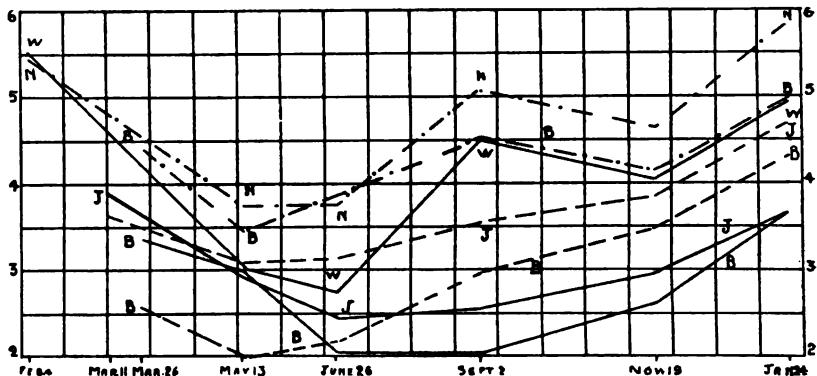


FIG. 3.—Graphs showing variation of ash in percentages of fresh weight

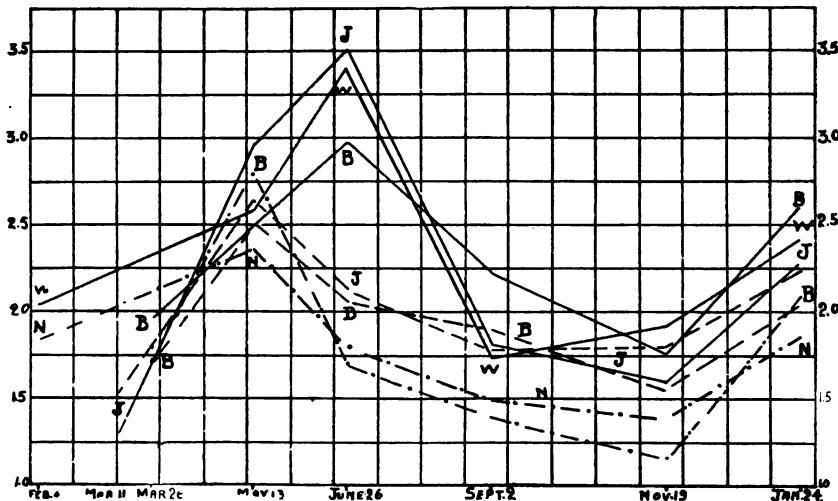


FIG. 4.—Graphs showing variation of titratable acidity in cubic centimeters of n/10 acid per gram of dry weight

uary, the minima in March and during the fall. For the other spurs the first maximum occurs in May. No determinations for acidity were made on Wealthy or Nixonite spurs between February and May but the values reached by these curves in January and the course of the other curves indicate clearly the existence of minima sometime in March. During the spring there is very little difference between the courses of the various curves until May, after which the bearing spurs increase in acidity while the others decrease. In June the greatest differences between the various types are to be found. Thruout the season the barren spurs are marked by their relatively low acidity.

The values for the titratable acidity in terms of fresh weight are given in Table 5, and the curves are shown in Figure 5. Comparison with Figure 4 shows considerable difference in the spring but the general shape of the curves is not materially different.

The potassium determinations are given in Table 6 and the graphical picture in Figure 6. In the early spring there is little

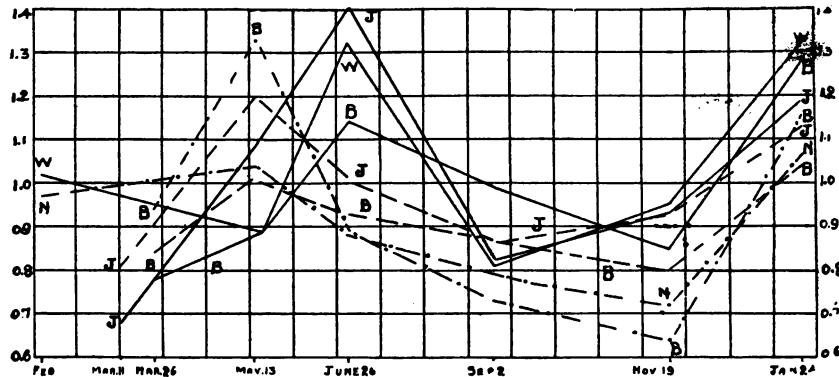


FIG. 5.—Graphs showing variation of titratable acidity in cubic centimeters of $n/10$ acid per gram of fresh weight

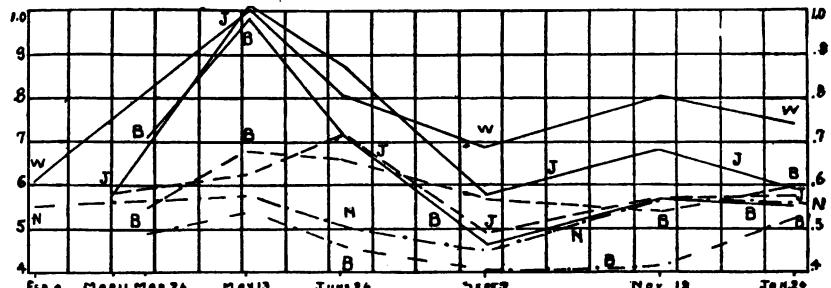


FIG. 6.—Graphs showing variation of potassium in percentages of dry weight

difference between the potassium content of the various types of spurs but during April and May the curves for the bearing spurs rise rapidly to a high value while those of the non-bearing spurs and the barren spurs increase to a much less extent. In the middle of May the difference in the potassium content of the three types of spurs is most marked. After May the potassium content decreases in the non-bearing spurs where it remains nearly constant or increases to a maximum in June. All the curves show a minimum in the fall. In January there is very little difference in the potassium content of the various types. The barren spurs have a low potassium content thruout the year while that of the bearing spurs is high.

The potassium determinations expressed in terms of fresh weight are given in Table 7 and represented graphically in Figure 7. This figure is on a larger scale than Figure 6, but the general

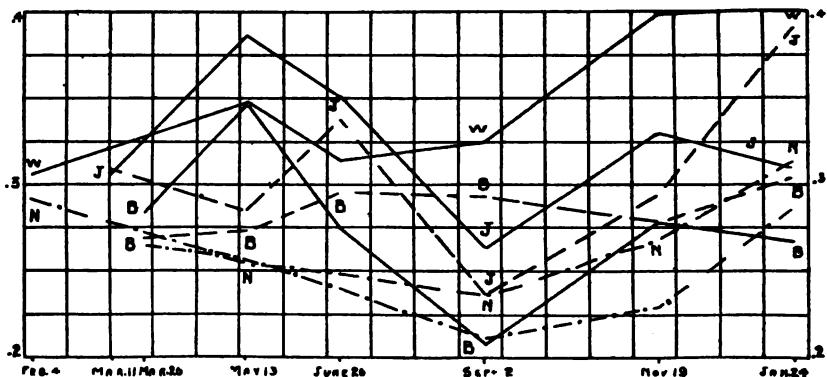


FIG. 7.—Graphs showing variation of potassium in percentages of fresh weight

shape of the individual curves is approximately the same. It will be noted that the curves for the non-bearing spurs rise during May and June.

The values for phosphorus in terms of dry weight are given in Table 8 and Figure 8. All the curves start from about the same position in February, whence the bearing spurs rise to a maximum in May while the non-bearing and barren spurs fall rapidly to a minimum at the same time. The curves come together again in June and have approximately the same values during the rest of the year. The barren spurs have the lowest values thruout the year.

The percentages of phosphorus in terms of fresh weight are

given in Table 9 and Figure 9. On the fresh weight basis the bearing spurs have a maximum in February or March and a minimum in June or later. The maximum shown by the dry weight curves in May is completely effaced. The curves for the barren and non-bearing spurs are similar in all essential respects to the curves in Figure 8.

The percentages of total nitrogen in terms of dry weight are given in Table 10 and Figure 10. The nitrogen content of the bearing spurs increases from March to May when a very high maximum is reached. During May and June the nitrogen content falls rapidly and during the rest of the year remains fairly constant with

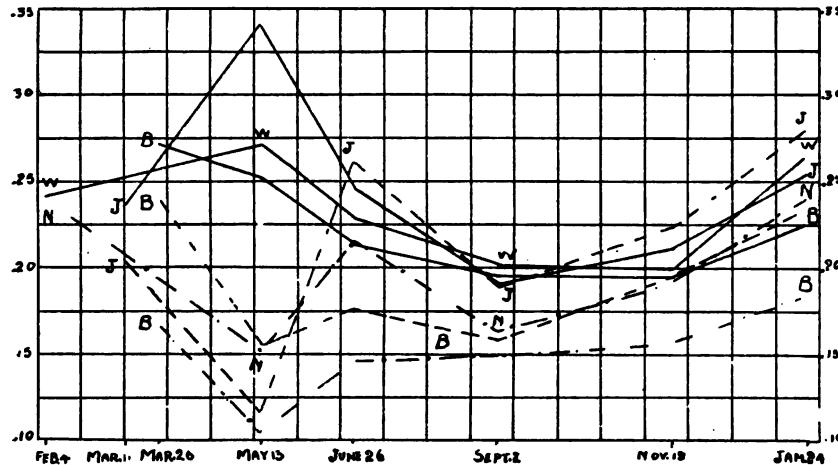


FIG. 8.—Graphs showing variation of phosphorus in percentages of dry weight

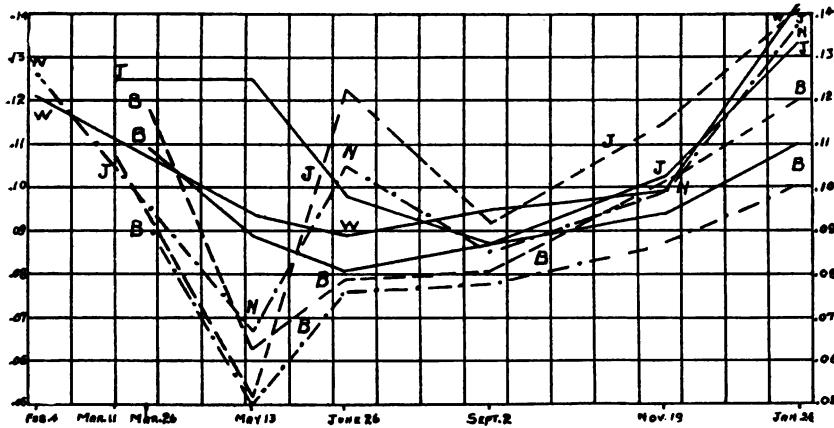


FIG. 9.—Graphs showing variation of phosphorus in percentages of fresh weight

a minimum in November. The non-bearing and barren spurs show a decrease in the percentage of nitrogen during the spring and reach a minimum in June. During the rest of the year the non-bearing spurs increase gradually in nitrogen content so that their curves cross those of the bearing spurs in November. In the winter those spurs which are to bear the coming season have a slightly higher nitrogen content than those which do not. The barren spurs are low in nitrogen throughout the year. The difference in nitrogen content of the bearing and non-bearing spurs in May is very marked.

The percentages of total nitrogen on the fresh weight basis are given in Table 11 and Figure 11. As in the phosphorus figure the

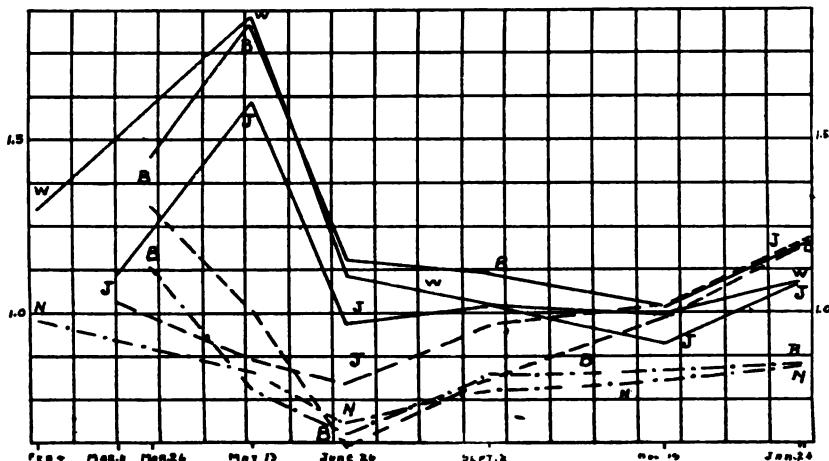


FIG. 10.—Graphs showing variation of nitrogen in percentages of dry weight

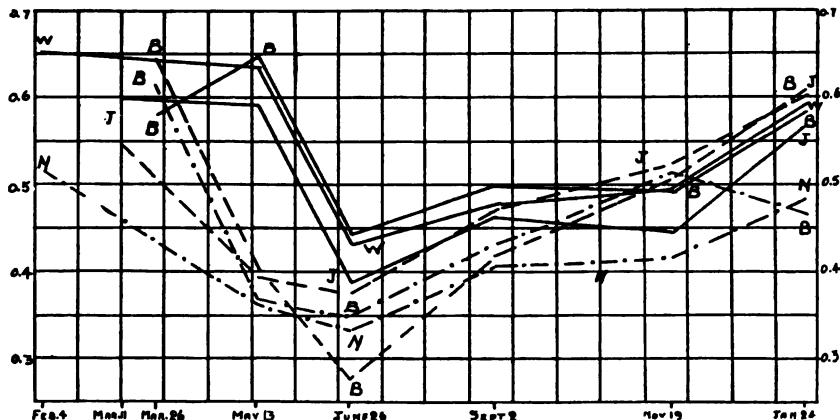


FIG. 11.—Graphs showing variation of nitrogen in percentages of fresh weight

maximum in the curves of bearing spurs which occurs in May is nearly effaced. It occurs only in the Ben Davis curve. In other respects the two pictures are similar.

The percentages of reducing sugars in terms of dry weight are given in Table 12 and Figure 12. The bearing and non-bearing spurs have a maximum content in the winter and a minimum content in May. The barren spurs have a minimum in June. Differences between the various types of spurs are not marked; however, the bearing spurs have less reducing sugar in May than the non-bearing or barren spurs. In the winter the spurs which are to bear have a lower content of reducing sugar than those which have

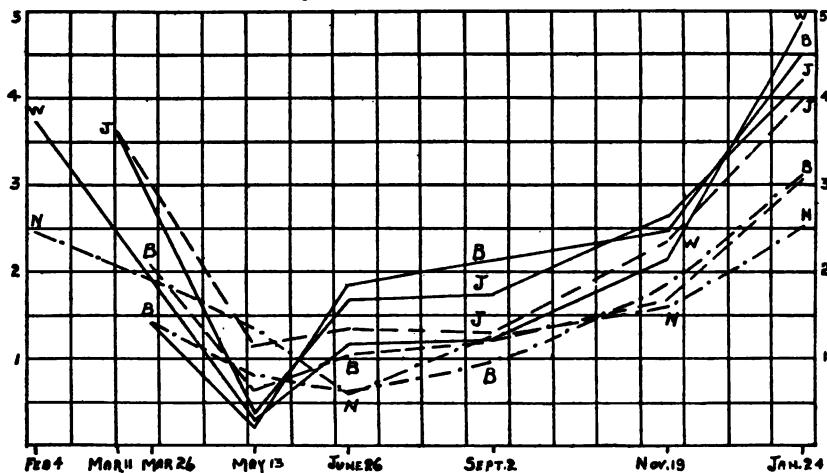


FIG. 12.—Graphs showing variation of reducing sugars in percentages of dry weight

borne, but a higher content than the barren spurs which are relatively low in reducing sugars throughout the year except in May.

The percentages of reducing sugars in terms of fresh weight are given in Table 13 and Figure 13. It will be noted that Figure 13 is practically identical with Figure 12.

The percentages of non-reducing sugars in terms of dry weight are given in Table 14 and Figure 14. These values are obtained by difference. The bearing spurs show a maximum content in November and the non-bearing and barren spurs in January. At other times the amount of non-reducing sugars present is relatively insignificant.

The percentages of total sugars in terms of dry weight are

given in Table 15 and Figure 15. The course of these curves is essentially the same as that of reducing sugars shown in Figure 12.

The percentages of total sugars in terms of fresh weight are given in Table 16 and Figure 16. The picture presented is essentially identical with that presented on the dry-weight basis and with that presented by the reducing sugars alone.

The percentages of starch in terms of dry weight are given in Table 17 and Figure 17. These curves are characterized by two maxima, one in March and the other in September and two minima,

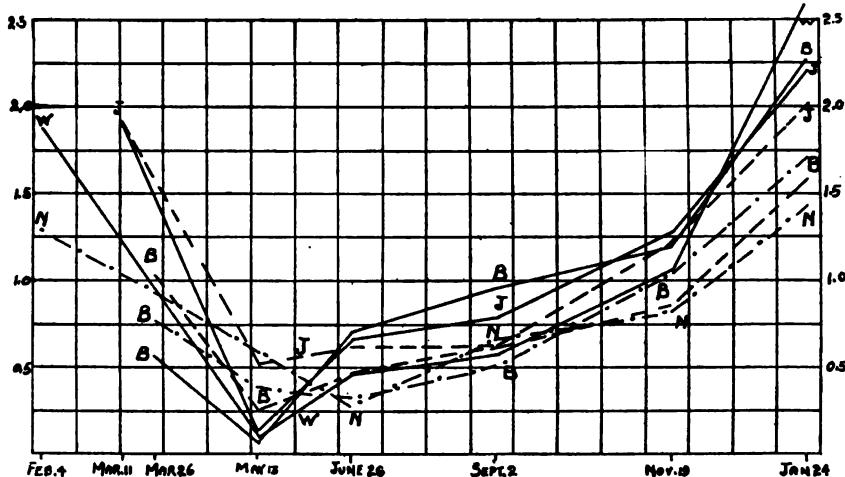


FIG. 13.—Graphs showing variation of reducing sugars in percentages of fresh weight

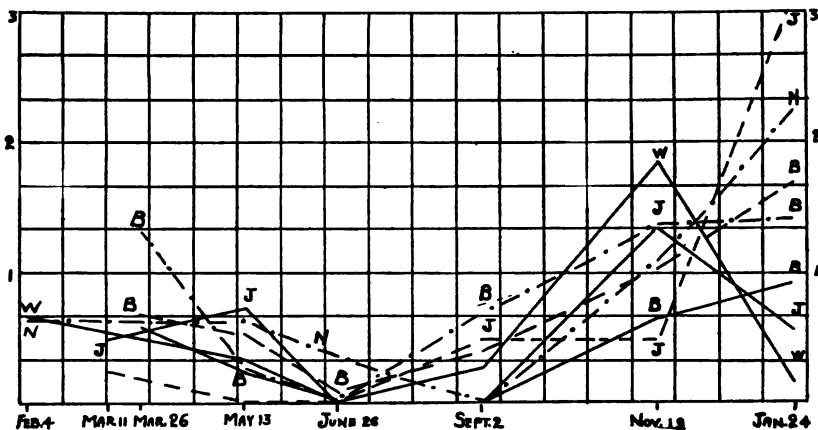


FIG. 14.—Graphs showing variation of non-reducing sugars in percentages of dry weight

one in May and the other in January. The bearing spurs lose practically all their starch by the middle of May and appreciable amounts are not in evidence in May or June, altho microchemical examination reveals the presence of a few starch grains during this period. After June the starch content rises rapidly to the maximum in September and then falls off during the fall and winter. The non-bearing spurs also have practically no starch during May but appreciable quantities are present in June which distinguishes these spurs from the bearing and barren spurs. During the winter the spurs which are to bear have slightly more starch than other spurs but the greatest difference occurs in June. The barren spurs

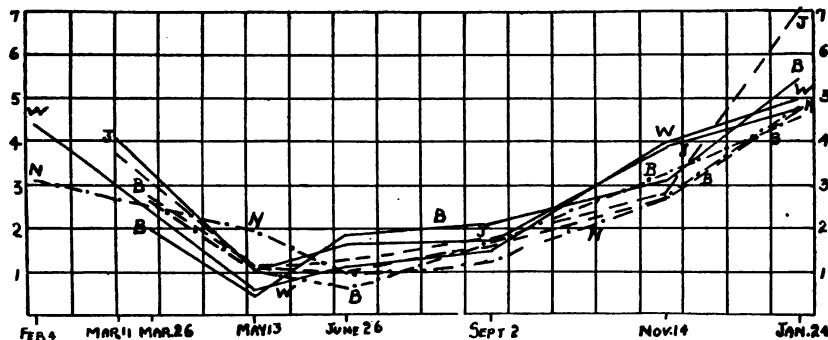


FIG. 15.—Graphs showing variation of total sugars in percentages of dry weight

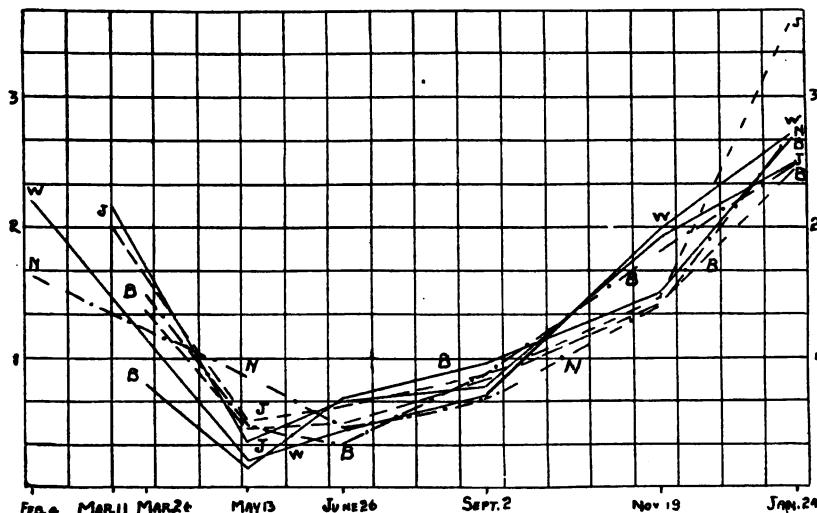


FIG. 16.—Graphs showing variation of total sugars in percentages of fresh weight

are low in starch thruout the year and have barely appreciable amounts in May and June.

The percentages of starch on the fresh-weight basis are given in Table 18 and Figure 18. There are no significant differences between this picture and that on the fresh weight basis.

The percentages of total polysaccharides less starch in terms of dry weight are shown in Table 19 and Figure 19. These curves

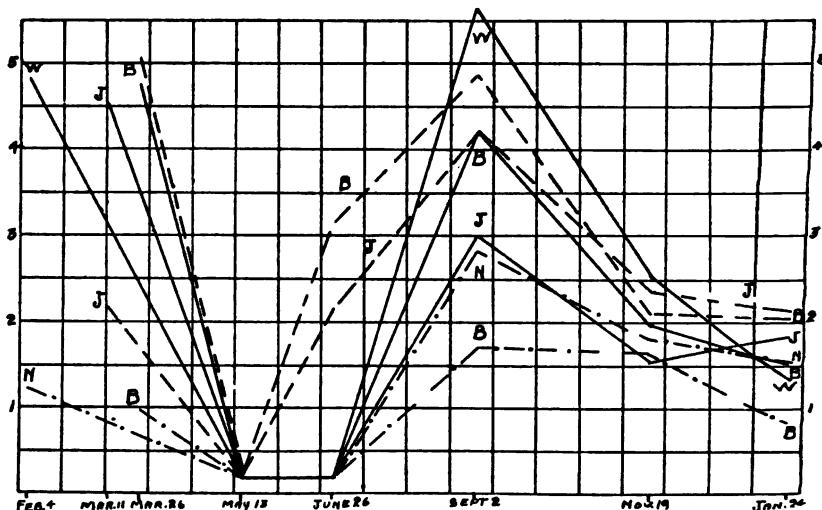


FIG. 17.—Graphs showing variation of starch in percentages of dry weight

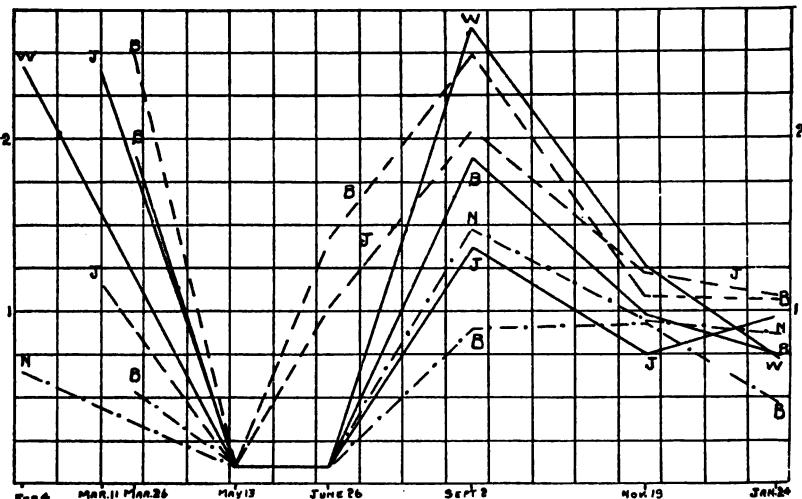


FIG. 18.—Graphs showing variation of starch in percentages of fresh weight

probably do not represent the variations in any one constituent, and consequently do not present the uniform picture presented by other constituents. The bearing spurs show a minimum in the winter and a maximum in September, with the exception of the Ben Davis spurs which reach a maximum in November or possibly sometime sooner. The non-bearing spurs show two maxima, one in May and the other in September with a minimum between them

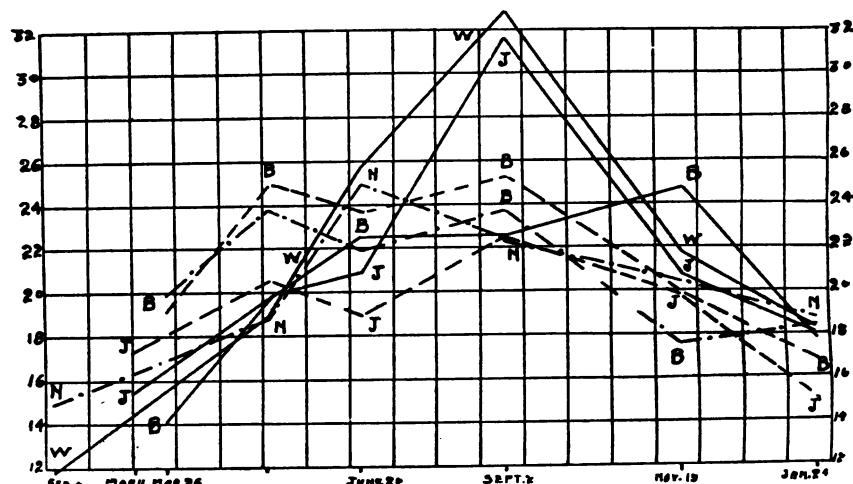


FIG. 19.—Graphs showing variation of polysaccharides other than starch in percentages of dry weight

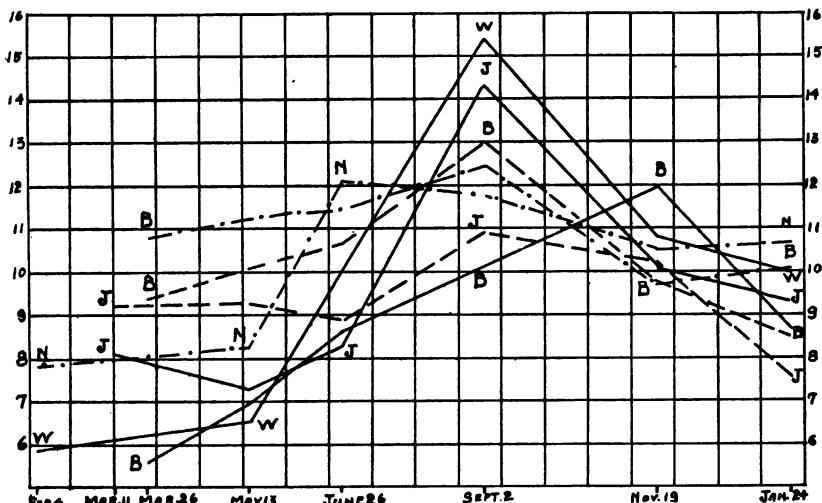


FIG. 20.—Graphs showing variation of polysaccharides other than starch in percentages of fresh weight

and another minimum in the winter. The barren spurs have curves more or less similar to those of the non-bearing spurs. During the winter those spurs which are to bear have a relatively low content. The greatest difference between the several types occurs in September but at no time is the distinction clear cut.

The percentages of total polysaccharides less starch in terms of fresh weight are given in Table 20 and Figure 20. On this basis all the spurs have a maximum in September with the exception of the bearing spurs of Ben Davis which have a maximum later, and the barren spurs of Nixonite which have a maximum early. In the bearing and non-bearing spurs the minimum occurs in January and

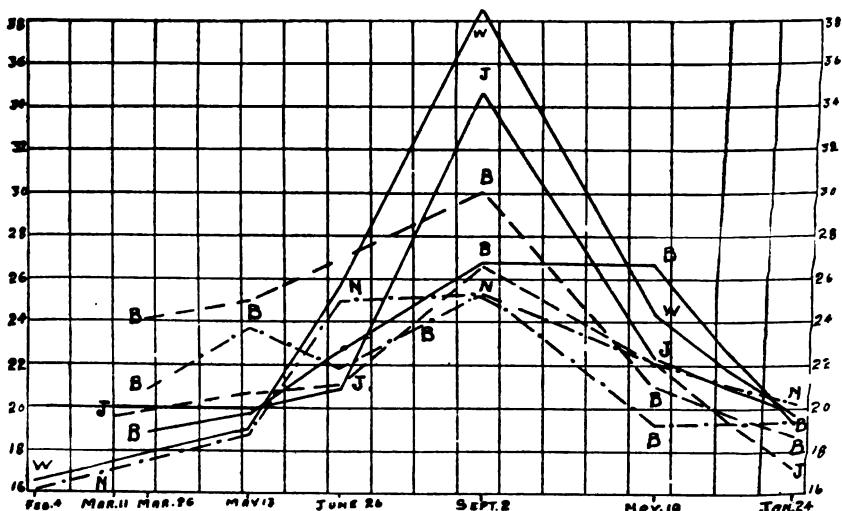


FIG. 21.—Graphs showing variation of total polysaccharides in percentages of dry weight

in the barren spurs in November. Thruout the season the values for the barren spurs are relatively high, for the non-bearing spurs intermediate in the spring and low in the winter and for the bearing spurs low in the spring and high in September.

The percentages of total polysaccharides in terms of dry weight are given in Table 21 and Figure 21. The general shape of the curves is not essentially different from those in Figure 19 except that the non-bearing spurs have a single maximum in September and a single minimum in January.

The percentages of total polysaccharides in terms of fresh weight are given in Table 22 and Figure 22. This figure is on a

smaller scale than the previous figure. The most significant difference occurs in May when the spurs show a minimum.

The percentages of total carbohydrates in terms of dry weight are given in Table 23 and Figure 23. These values do not include crude fiber. The figure is essentially similar to Figure 21 except that the bearing and non-bearing spurs have a minimum in May. The most striking differences among the three types of curves occur in September when the bearing spurs show an exceptionally high carbohydrate content. At this time the barren spurs have a relatively low carbohydrate content and the non-bearing spurs are intermediate. In January there are no pronounced differences

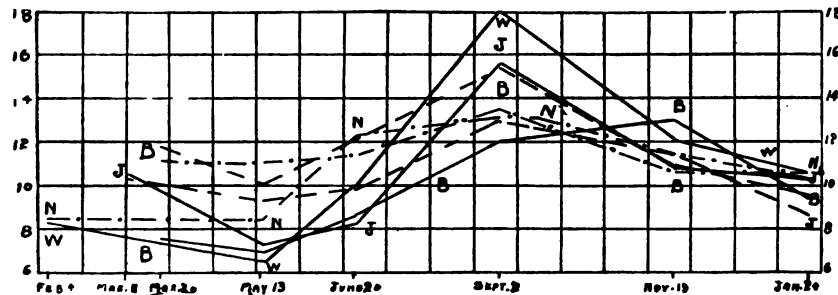


FIG. 22.—Graphs showing variation of total polysaccharides in percentages of fresh weight

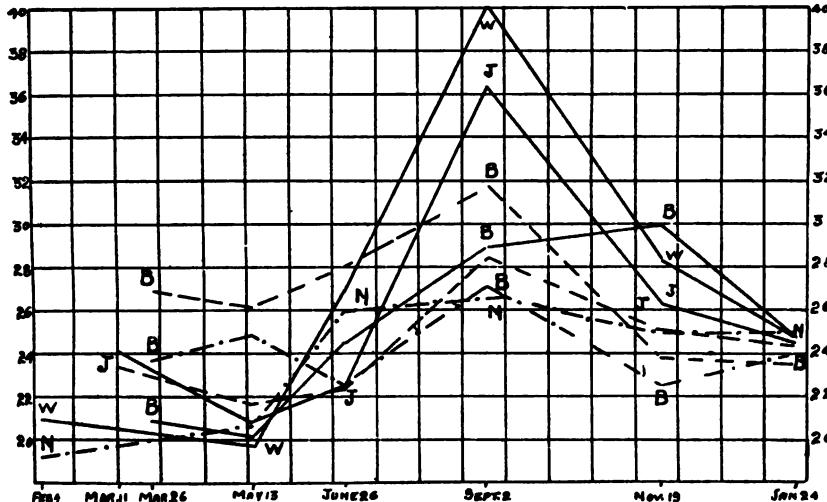


FIG. 23.—Graphs showing variation of total carbohydrates in percentages of dry weight

among the various types altho the spurs which are to bear the following year have a lower carbohydrate content than other spurs.

The percentages of total carbohydrates in terms of fresh weight are given in Table 24 and Figure 24. This figure is practically identical with Figure 22 the percentages of total polysaccharides in terms of fresh weight.

The hydrogen ion concentrations are given as pH in Table 24. The differences between the various types of spurs as obtained by the method used are not striking. In general the bearing spurs show an increased acidity in the spring with a maximum hydrogen ion concentration in May and a minimum in November. The non-bearing spurs show a minimum hydrogen ion concentration in September and a maximum in March. More refined methods are probably required for the determination of hydrogen ion concentration.

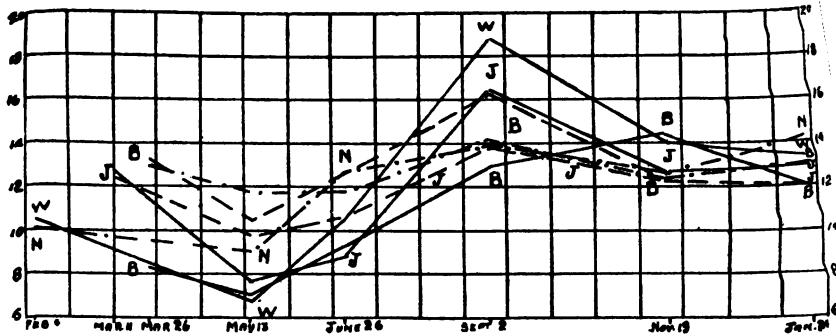


FIG. 24.—Graphs showing variation of total carbohydrates in percentages of fresh weight

DISCUSSION

The most striking feature of the data just presented is the uniformity with which the chemical composition of the spurs of a single type, regardless of variety, varies throughout the year. Thus we find that the bearing spurs have curves which all show much the same general characteristics, and so also the non-bearing and barren spurs. This is particularly noticeable in the determinations of dry weight, acidity, potassium, phosphorus, nitrogen and starch. In fact, all the graphs show distinctive features in the curves for at least one type of spur. Thus the ash content of bearing spurs drops during May and June, and the decrease in the sugar content of bearing spurs falls to an extreme minimum in May, altho the percentage

centages of sugar are essentially the same in all types of curves. As a rule the determinations for bearing spurs assume one extreme value, those for the barren spurs the other extreme, while the non-bearing spurs have for the most part an intermediate position. This is the case thruout the greater part of the course of the curves showing dry weight, acidity, potassium, nitrogen, phosphorus, reducing sugars and starch. In the case of the percentages of ash the barren spurs have values which run during the first part of the year more or less parellel with those of the bearing spurs and during the latter part of the year with those of the non-bearing spurs.

In general, however, barrenness of the tree, regardless of variety is characterized by a seasonal chemical picture in the spurs distinctly different from that of a bearing tree, whether we consider its bearing or non-bearing spurs, or its bearing or non-bearing years. Barrenness or productivity is thus shown to be an expression of chemical condition or chemical equilibrium within the tree, as is also the alternation of off year and bearing year. It should be borne in mind that at the time of sampling it was sometimes impossible to draw a hard and fast line between bearing and non-bearing spurs or to select spurs that could definitely be predicted to develop fruit buds, or to remain barren. In some instances, therefore, the samples analyzed represent a collection of spurs the great majority of which could reasonably be expected to be bearing, non-bearing, or barren, as the case might be. Since this is the case, the actual differences existing between the three types of spurs studied are probably greater than are shown by the data presented.

It is also particularly significant that in most cases marked differences occur in the composition of the various types of spurs as regards any one given constituent at one season of the year, while at other times no marked differences between the various types may be in evidence. Thus, for example, large differences in the dry weight occur in May, in acidity in June; in potassium, phosphorus and nitrogen in May, while the starch content of the non-bearing spurs in June is especially striking. From this it is evident that determinations calculated to reveal differences in chemical composition corresponding to differences in physiological behavior or morphological structure cannot be made at any and every season of the year.

If this correspondence holds then certain elements and compounds are of special significance in the question of productivity at certain seasons of the year, while at other times they are not all-

important controlling factors. In some of the early experimental work in this field, determinations were made in the fall or winter when differences in the content of many constituents, especially potassium, total sugars, total carbohydrates and even starch, are at a minimum.

Dry Weight.—A study of the variations in dry weight shown in Figure 1 discloses a rapid decrease in percentage during the spring which is probably to be accounted for largely by an increase in the amount of moisture rather than by a decrease in the absolute amounts of dry material. Comparison with the total carbohydrate figures shows that the decrease of this constituent in bearing and non-bearing spurs plays but a small role in the total decrease in percentage of dry matter, while the barren spurs actually increase in total carbohydrate content at this time. It may be concluded therefore that blossoming spurs absorb more water in the spring than non-bearing or sterile spurs. The increase in percentage of dry material which occurs in all types of spurs from May to September is probably due in large part to the increase in carbohydrate. After September the percentage of dry material remains fairly constant, increasing in some cases and decreasing in others. At this time there is a decrease in the percentage of total carbohydrates in all types of spurs and consequently the percentage of dry material is probably maintained by loss of moisture.

Ash.—The most striking feature of the picture presented by the ash determinations is the rapid decrease in the percentage of ash in bearing spurs at the time when fruit is developing. The curve for the Wealthy spurs runs more nearly parallel with the curves for the barren spurs than for those of the other bearing spurs. This may perhaps be correlated with the fact that the apples were picked from the Wealthy spurs in the summer while the Jonathan and Ben Davis spurs still carried apples when the September samples were collected. It will be noted that in every case the ash content of the bearing spurs increases after the apples are removed, so the natural assumption is that ash constituents are being withdrawn from the spur to the fruits as long as they are attached. The non-bearing spurs show a gradual accumulation of ash constituents from June on, so that in winter these spurs which will bear the following season have a higher ash content than those spurs that have just borne. Altho the ash content of barren spurs is high thruout the year, this is not due to the more

important ash constituents, potassium and phosphorus, as reference to their figure shows.

Titratable Acidity.—The curves showing the titratable acidity are characterized by having two maxima. This condition occurs in only one other set of curves, those for starch, thus suggesting that titratable acidity and starch content are related. For comparison average curves showing the acidity, starch and reducing sugar content of bearing and non-bearing spurs are given in Figures 25 and 26 respectively. It will be noted that the maxima in the starch curves correspond with the minima in the acidity curves and the

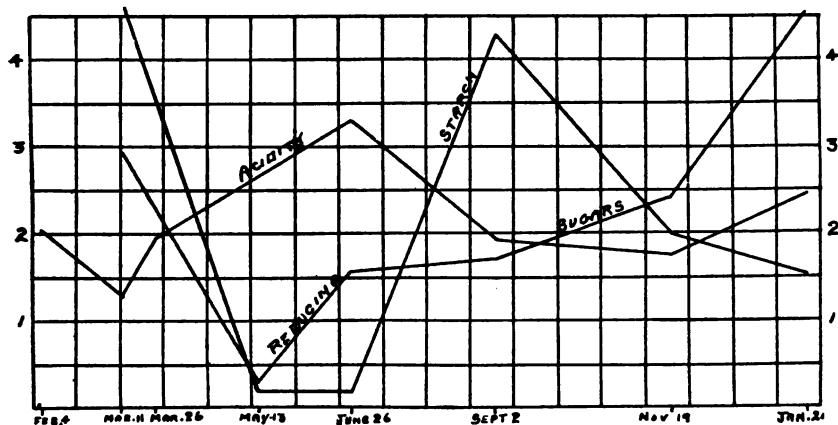


FIG. 25.—Graphs showing average variation of titratable acidity, non-reducing sugars and starch for bearing spurs in percentages of dry weight

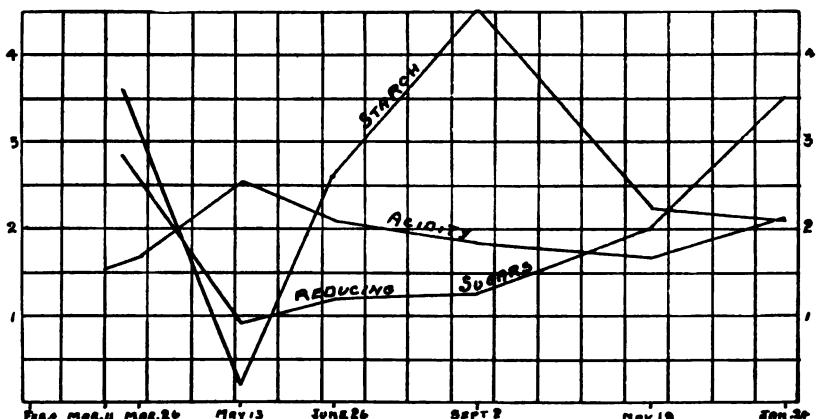


FIG. 26.—Graphs showing average variation of titratable acidity, non-reducing sugars and starch for non-bearing spurs in percentages of dry weight

minima in the starch curves correspond with the maxima in the acidity curves. The rapid increase of acidity which occurs in all types of spurs from March to May corresponds with a decrease in the percentages of starch and sugars, both of which constituents are very nearly exhausted by the middle of May. If we assume that the starch is broken down to sugar and that the sugar is incompletely oxidized leaving a residue of organic acids, the situation which occurs in bearing and non-bearing spurs is explained. If this is the correct interpretation the amount of titratable acidity in the spur may be taken as an index of recent catabolic activity. It is interesting to note that the bearing spurs which are producing fruit from May to June show an increase in titratable acidity while the non-bearing and barren spurs show, at this time, a decrease.

Potassium.—The curves showing the variations in bearing spurs of potassium, phosphorus and nitrogen are characterized by sharp rises in the spring to a very high maximum in May. After May there is an abrupt decline to a minimum value in September to November. That this condition is in some way associated with the fact that these spurs blossom and bear fruit is rendered most probable by its absence in non-bearing and barren spurs.

The potassium content of all types of spurs increases in the spring but this increase in the case of non-bearing and barren spurs is not marked while in the case of bearing spurs it is an increase of almost 66 per cent. In the period from May to June the percentage of potassium decreases in both bearing and barren spurs, while in the case of non-bearing spurs there is in one case a slight drop and in the other an actual rise. This period represents the beginning of fruit-bud differentiation in these spurs. The extremely low potassium content of barren spurs at this critical time, suggests that potassium starvation may be a factor in suppressing fruit-bud differentiation in this type of spur. As repeated attempts have been made to correlate potassium content with carbohydrate manufacture, it may be worthy of note that the relative potassium content of the various spurs in September corresponds very nearly with their relative total carbohydrate content, altho the latter is at this time at a maximum while the former is at a minimum.

Phosphorus.—The general similarity between the phosphorus and nitrogen curves has already been indicated (see Figures 27 and 28). This parallelism is more or less to be expected since both of these elements enter into the composition of nucleo-proteins.

Butler, Smith and Curry¹¹ found a similar parallelism in the vegetative shoots, where the variations in nitrogen and phosphorus content resemble those of non-bearing and barren spurs. However,

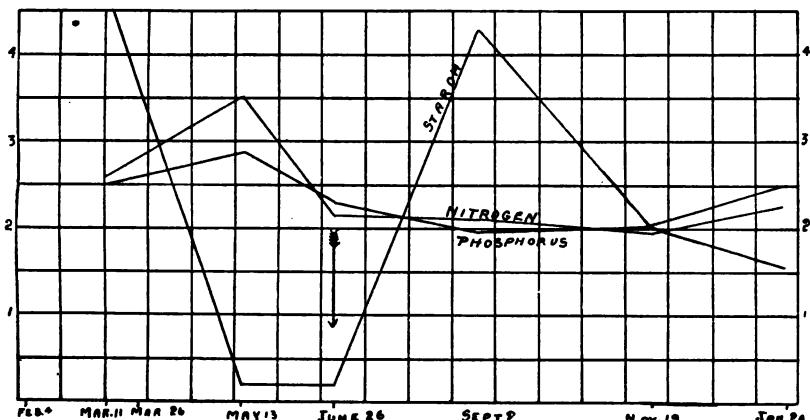


FIG. 27.—Graphs showing average variation of phosphorus, nitrogen and starch for bearing spurs in percentages of dry weight. The percentages of phosphorus are multiplied by ten and those of nitrogen by two for the sake of comparison. The arrow indicates the relative position of the starch and nitrogen curves during the period when fruit-bud differentiation would occur

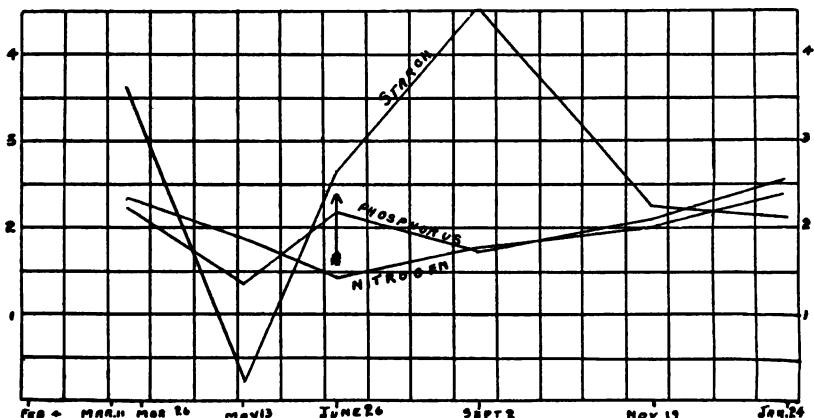


FIG. 28.—Graphs showing average variation of phosphorus, nitrogen, and starch for non-bearing spurs in percentages of dry weight. The percentages of phosphorus are multiplied by ten and those of nitrogen by two for the sake of comparison. The arrow indicates the relative position of the starch and nitrogen curves during the period of fruit-bud differentiation

11. Butler, O. R. et al. loc. cit. pp. 7 and 8.

the phosphorus content of the non-bearing and barren spurs increases in May and June after which it declines, while the nitrogen content decreases to a minimum at the end of June and increases thereafter. The close parallelism of the phosphorus curves for non-bearing and barren curves, particularly at the time of fruit-bud differentiation, suggests that phosphorus is not a significant factor at this season. However there is a marked accumulation of phosphorus in non-bearing spurs after September. During this period the curves for barren spurs are lower, which indicates that phosphorus storage may be an important factor in spurs that have developed fruit-buds, perhaps supplying the demands for phosphorus during the early development of the seeds and fruits. This is supported to some extent by the increase in the phosphorus content of bearing spurs during the early spring, in sharp contrast to the condition in non-bearing and barren spurs.

Nitrogen.—The relative amounts of nitrogen in bearing and non-bearing spurs at the end of June is particularly interesting in connection with the discussion of the carbohydrate-nitrogen ratio. As has already been mentioned the end of June is the time when fruit-bud differentiation is taking place in the non-bearing spurs. At this time the nitrogen content of the non-bearing spurs is very much less than that of the bearing spurs where no fruit-bud differentiation is taking place. However, the nitrogen content of the barren spurs is also low at this time and yet no fruit-bud differentiation occurs. Consequently, the decisive factor for fruit-bud differentiation must be found elsewhere. An examination of the total carbohydrate curves fails to show any clear-cut difference at this time between bearing and non-bearing spurs, but the curves for starch are highly significant in this connection. At the end of June an appreciable amount of starch has accumulated in the non-bearing spurs while in both bearing and barren spurs appreciable quantities of starch are still absent. It would therefore seem that the starch-nitrogen ratio or the amount of starch alone was the most indicative factor at the time of fruit-bud differentiation. For comparison average starch and nitrogen curved of bearing and non-bearing spurs are shown in Figures 27 and 28, respectively. The percentages of nitrogen have been doubled in both cases for convenience.

Since starch is an inert substance it is difficult to conceive that the amount of starch bears any direct causative relation to the differentiation of fruit-buds. However the factors that are asso-

ciated with starch accumulation may also be decisive for fruit-bud differentiation and in this way the starch-nitrogen ratio acquires significance. The determining factors are more probably of the nature of acidity and concentration. It is worthy of note that a combination of relatively low acidity and relatively high sugar content at the time of fruit-bud differentiation occurs only in non-bearing spurs.

Like phosphorus, the nitrogen content of bearing spurs increases markedly in the spring, an increase of approximately 50 per cent, while the nitrogen content of other spurs decreases during this time. This might indicate one of the three things; that different amounts of nitrogen were available to the different trees; that nitrogen passed from the non-bearing to the bearing spurs on the same tree; or that the available nitrogen was taken up differentially by the bearing spurs. It is unlikely that different amounts of available nitrogen should be at the disposal of the various trees since they are all growing in the same orchard under the same conditions in close proximity to one another. Moreover, the samples of bearing and non-bearing spurs of Jonathan were taken from the same tree and the analyses of these spurs show that they behave in the same way as the bearing and non-bearing Ben Davis spurs which were collected from separate trees, one in heavy bearing and the other in the off year. It is also impossible that the increase in the nitrogen content of the bearing spurs should be supplied by the non-bearing spurs, since in the cases of both Wealthy and Ben Davis the vast majority of the spurs bore the year the samples were taken. So it would seem more probable that the nitrogen of the bearing spurs comes from a source which is at the disposal of the non-bearing spurs but is not used by them. This source of nitrogen may be the nitrates of the soil or some reserve supply of stored nitrogen. Several facts lend support to the latter hypothesis. One is the large increase in the nitrogen content of bearing spurs in the early spring, which is so great that the soil supply would seem insufficient to account for it.

Whiting and Schoonover¹² give the relative rates of nitrate production in the soil at different seasons of the year in the following order: (1) Late spring and early summer; (2) early autumn; (3) summer and (4) winter. They state that "no evidence of nitrate production has been found in the winter." It follows there-

12. Whiting, A. L. and Schoonover, W. R. Nitrate production in field soils in Illinois. Ill. Agr. Exp. Sta. Bul. 225: 60, 61. 1920.

fore that the nitrate supply in the soil must be at a minimum in the early spring when the nitrogen content of bearing spurs rises to its maximum. Furthermore the trees studied are growing under sod and Gourley and Shunk¹³ give evidence that "nitrates are reduced to a minimum under sod to a marked degree as compared with the same soil under tillage." The nitrogen content of non-bearing spurs increases steadily from June to January as also the phosphorus content, so that at the beginning of the growing season the spurs which are to bear have a slightly higher nitrogen content than other spurs. If this gradual increase in nitrogen content, at a time when there is an available nitrate supply in the soil, may be taken as an indication of the accumulation and possibly the storage of nitrogen thruout the tree, it is conceivable that a reserve supply of elaborated nitrogen is present and can be drawn upon by the bearing spurs in the spring. This would account for the source whence the nitrogen of bearing spurs is derived as well as for the magnitude of the increase in the early spring, which may be a temporary accumulation used in the development of the seeds. A similar state of affairs has been pointed out in connection with the phosphorus content. Relatively large amounts of nitrogen and phosphorus are needed for the seeds, and after May when they begin to develop the nitrogen and phosphorus content of the bearing spurs drops rapidly. The whole question of nitrogen elaboration, nitrogen storage and nitrogen utilization can be settled only by further investigation, and work with this point in view is now under way.

The nitrogen content of barren spurs is low thruout the year and the gradual accumulation observed in non-bearing spurs from June to January does not take place, so that in the winter they have a markedly low nitrogen content. This may have some relation to the barrenness of these spurs, and lends weight to the assumption that nitrogen feeding and storage in the fall is a necessary antecedent to the productive condition.

Reducing Sugars.—The rapid decrease in the percentage of reducing sugars which occurs in all types of spurs from March to May has already been mentioned. The most rapid rate of decrease occurs in the bearing spurs which produce both leaves and blossoms during this period. The high rate of respiration in floral parts is well known and may account for the rapid consumption of re-

13. Gourley, J. H. and Shunk, V. D. Notes on the presence of nitrates in orchard soils. N. H. Agr. Exp. Sta. Tech. Bul. 11: 23. 1916.

ducing sugars at this time. In non-bearing spurs the rate of sugar consumption is less but in the barren spurs it is at a minimum, which may be correlated with the fact that these spurs show less vegetative activity than the non-bearing spurs. The minimum in the reducing sugar curve for barren spurs does not occur until June. In both the bearing and non-bearing spurs, however, the percentages of reducing sugars increase after the middle of May, which may be taken as an indication that photosynthetic activity is in excess of carbohydrate utilization. The acidity curve for the bearing spurs suggests that catabolic reactions are still going on in these spurs from May thru June. The sugar content of all types of spurs increases from September to the end of January. This increase can hardly be accounted for by photosynthetic activity. Undoubtedly this increase in sugar represents a digestion of starch and possibly other polysaccharides which decrease in amount during this period. The similarity in the general shape of the reducing-sugar curves and the dry-weight curves is worthy of note, as is also the similarity of the reducing sugar curves on the fresh- and dry-weight bases. This is probably due to the fact that the percentages of reducing sugars are at a minimum at the same time as the percentages of dry weight.

Non-reducing Sugars.—The curves showing the variations and percentages of non-reducing sugars are rather irregular. It will be noted, however, that at no time except during the winter are the amounts of non-reducing sugars large in proportion to the amounts of reducing sugars. As a result the curves for total sugars are practically identical with the curves for reducing sugars only. The chief difference occurs in the winter when appreciable amounts of non-reducing sugars are present in non-bearing and barren spurs. These probably represent reserve supplies of stored carbohydrate.

Starch.—The variations in starch content have already been discussed to some extent and emphasis has been laid on the accumulation of starch in non-bearing spurs in May and June. It should be noted in this connection that practically all of the analyses which have been made by previous investigators to determine relative amounts of starch in various plant tissues have been in reality analyses of total polysaccharides. Thus for example Butler, Smith and Curry¹⁴ give analyses for starch that are evidently total polysaccharides, thus vitiating their conclusions on carbohydrate metabolism. In many succulent plants, no doubt, starch

¹⁴. Butler, O. R. et al. loc. cit. page 4, Table 1.

represents the major part of the total polysaccharides present but in the case of the fruit spurs of the apple the amount of total polysaccharides is from six to ten times that of starch. This explains why various investigators have found marked differences in the starch content of bearing and non-bearing spurs when determinations were made microchemically with the use of the iodine test but were unable to corroborate these results by quantitative analysis. Thus, for example, Gourley¹⁵ states that "While both twigs contained considerable starch yet the one which had formed the fruit buds was furnished with a very much larger amount than where leaf buds only were formed. The twigs themselves were a little larger as will be seen by the photograph, but the cells of the storage tissue, pith and medullary rays, were practically all filled up, while in the other case there were many sections which showed very little or none in the central pith and often the secondary medullary rays within the bundle showed practically no deposit." (Page 59.)

"A chemical determination was made to ascertain definitely the difference in the amount of carbohydrates in the two cases but the method used was evidently unsatisfactory as no differences were obtained. It is likely that some of the tissue was oxidized as well as the carbohydrates. The method used is here given however as a matter of record." (Page 67.)

The fact that starch represents the major portion of the total polysaccharides in annual plants, probably accounts for the use of the term carbohydrate-nitrogen ratio, but as has already been pointed out, the starch-nitrogen ratio is more important and is a more nearly accurate measure of the conditions determining fruit-bud differentiation, at least in the apple.

The percentages of starch decrease in all types of spurs after September. This decrease may be in part due to the transformation of the starch into sugars. These sugars may be either carried to other portions of the plant or stored in the spurs themselves in the form of non-reducing sugars, or they may remain in the spurs without undergoing change. The increase in the percentages of the reducing and non-reducing sugars shows that a considerable portion if not the major part of the starch remains in the spurs in the form of sugar. During the winter it will be noted that non-bearing spurs which will bear fruit the following season have a higher percentage of starch than those spurs which have just borne

15. Gourley, J. H. Studies in fruit bud formation. N. H. Agr. Exp. Sta. Tech. Bul. 9: 59, 67. 1915.

fruit. This corroborates the microchemical findings of Gourley.¹⁶ The existence of two maxima in the starch curve corroborates the microscopic studies of Mer¹⁷ and d'Arbaumont.¹⁸

Polysaccharides.—Figures 19 and 20 show the variations in the percentages of total polysaccharides less starch. These values probably do not represent any one compound although they may be considered as indicating roughly the variations in pentosans and allied substances. Large amounts of pectin are present in the spurs, and the starch storage cells which occupy the pith have middle lamellae which give a red color with concentrated hydrochloric acid and phloroglucinol. During the spring there is an increase in the percentages of these polysaccharides in all types of spurs. This increase probably represents the deposition of permanent cell wall structures and accounts in part for the utilization of starch and sugars which occur at this time. After May the percentages of these compounds increase in bearing spurs to a very high maximum in September. Whether this can be related to the development of specialized tissue in the purse can only be determined by further investigation. In non-bearing spurs the percentage of these polysaccharides decreases during May and June and reaches a minimum about the middle of the period of fruit-bud differentiation. Of the barren spurs, the Nixonite show an increase and the Ben Davis show a decrease during May and June. After September the polysaccharide content of all spurs decreases except in the case of the bearing Ben Davis spurs which do not show a maximum until November. In these spurs a higher maximum may have occurred at some time between September 2 and November 19, but as no analyses were made in this interval the question cannot be settled. This decrease in polysaccharides during the fall and winter may be in part the result of hydrolysis to sugars which increase during this period, but this will not account for the total decrease which is found to occur.

The slight difference which exists between the curves for total polysaccharides and polysaccharides less starch is striking evidence of the small proportion of starch present and emphasises the necessity for accurate starch determinations in this type of work.

Total carbohydrates.—The curves for total carbohydrates cor-

16. Gourley, J. H. loc. cit. Plates I and II.

17. Mer, E. Des variations qu' éprouve la réserve amyacée des arbres aux diverses époques de l'année. Bul. soc. bot. 45: 299. 1898.

18. d'Arbaumont, J. Sur l'évolution de la chlorophylle et de l'amidon dans la tige de quelques végétaux ligneux. Ann. sci. nat. Bot. Ser. 8. 13: 319-423; 14: 1-5-212. 1901.

respond in general with the curves given by Leclerc du Sablon¹⁹ for the total carbohydrate content of the chestnut, and pear, altho these latter curves show a maximum in October instead of September. The very slight difference in total carbohydrate content of the various types of spurs at the end of January is particularly noticeable.

INTERPRETATION

Vigorous apple spurs usually pass thru a two-year cycle; one year they bear, the other they do not. The chemical picture of this complete cycle can be seen from the data presented by considering the curves for bearing spurs as direct continuations of the curves for non-bearing spurs. Strictly speaking this involves an error, since the samples at the beginning of each series comprise one year's growth while at the end they comprise two years' growth. In most instances, however, this error is negligible since the correspondence between the end of the non-bearing curves and the beginning of the bearing curves is on the average very close, as is also that between the end of the bearing curves and the beginning of the non-bearing curves.

A picture of the chemical life-history of an apple spur during this two-year cycle will serve as a fitting review of the previous discussion, and if some of the statements are more or less conjectural, the main features are simply assertions of facts shown by the data already presented.

Starting with a spur in the off year, it contains slightly less ash including potassium and phosphorus, less nitrogen and less starch than a spur at the beginning of the bearing year, but it is higher in dry weight, reducing sugars and polysaccharides. During the spring, water is absorbed, the stored starch is hydrolyzed to sugar and the sugar is utilized along with phosphorus and nitrogen in the production of new growth. During this period of utilization of reserves and production of new vegetative tissue, the acidity and polysaccharide content, and to some extent the potassium content increase. Eventually, the supply of available carbohydrates is reduced to a minimum whereupon terminal bud formation takes place on spurs. After this, growth practically stops, which is accompanied by a falling off of acidity and polysaccharide content. By the photosynthetic activity of the newly formed leaves, a fresh supply of reducing sugar is formed some of which is stored in the

19. Leclerc du Sablon. loc. cit.

form of starch and other polysaccharides, resulting in an increase of dry weight. At the same time the potassium and phosphorus content increase somewhat, while the nitrogen content continues to fall off. As a result of conditions leading to high starch and low nitrogen content, fruit-bud differentiation occurs.

During the rest of this season, the spur gradually loses moisture. There is a steady accumulation of ash, nitrogen and later of phosphorus, indicating elaboration of nitrogen and phosphorus compounds in the leaves with storage in the spur and probably in other parts of the tree. As the leaves continue their photosynthetic activity the starch and other polysaccharides increase to a maximum. Later they decrease in amount, the products of hydrolysis augmenting the sugar content. The acidity continues to decline until the winter when it rises.

The spur then contains considerable stored material as is shown by the ash, phosphorus, nitrogen, non-reducing sugars and starch content, which are higher than they were the previous winter. Reducing sugars, polysaccharides, dry weight and acidity are relatively low. In the latter part of the winter, starch seems to be resynthesized and the acidity decreases to some extent.

During the second spring the spur blossoms and this involves an even fuller carbohydrate utilization than occurred the previous year, so that the exhaustion of the available carbohydrate supply at the time of terminal bud formation on spurs is more nearly complete. Meanwhile, the moisture, potassium, phosphorus and nitrogen content increased to a high maximum, previous to the development of the seeds and fruit.

The production of new tissue continues after terminal bud formation, and the photosynthetic products of the new leaves are utilized, so that the acidity and polysaccharide content continue to increase. The development of the young fruit and particularly of the seeds draws upon the nitrogen, potassium, phosphorus, and in fact the total ash content of the spur, which then falls rapidly. As a result of the absence of conditions leading to starch accumulation and a high nitrogen content, no fruit-buds become differentiated.

Later, the acidity falls off, sugar and eventually starch accumulate, and after the removal of the fruit the ash content increases. The polysaccharide content rises to a very high maximum, perhaps because of the development of specialized tissue in

the purse, but in the fall the starch and polysaccharide contents decrease.

In the winter, at the end of the two-year cycle we have the same condition with which we began. The spur is relatively high in dry weight, acidity, reducing sugars and polysaccharides, but relatively low in reserve material, starch, non-reducing sugars and ash.

APPLICATION

The previous discussion has shown the feasibility of correlating chemical composition with physiological state in the fruit spur of the apple. It is reasonable to suppose that similar correlations can be found in other parts of the tree. In many cases, differences in chemical composition lend themselves readily to physiological interpretation. In other cases, altho marked differences are present, no simple explanation is apparent but questions are suggested for further investigation.

The data presented are a step toward an understanding of normal conditions in what have been termed bearing, non-bearing and barren spurs. Further substantiating data are needed before these norms may be considered established, but the results so far obtained clearly show their existence. Some light has been thrown on the relationship of various chemical constituents which appear to be important at the time of fruit-bud differentiation and on other relationships which occur during the winter rest period, blossoming and the period of fruit development. Certain constituents such as phosphorus, nitrogen and starch seem to be particularly significant with reference to the present discussion, while others such as the sugars show differences which are at no time particularly striking, altho the slight differences observed may increase in importance as our knowledge of the significance of the variation and inter-relationship of these constituents becomes more comprehensive. Furthermore, notable differences occur at definite times of the year, and at other times no markedly distinguishing features are to be expected.

Perhaps this investigation has not gone far enough to warrant attempts toward direct practical application of the data secured, or to suggest modifications in established horticultural practices and standard orchard operations. However, it suggests several lines of further investigation by the same method of attack, which may in their turn throw considerable light on the general question of

tree nutrition and may in the end lead to definite modifications of orchard practice.

The bearing apple spur of trees with typically alternate bearing spurs has a chemical life-history distinct both from the spur preparing for fruit production and from the spurs of characteristically barren trees. Other investigators have pointed out that spurs lose their ability to bear every other year as they grow old and fruit at irregular and longer intervals, eventually reaching a condition superficially comparable to that of spurs on a barren tree. Is there also a change in the chemical life-history of aging spurs, tending toward that of spurs on barren trees? Can the chemical composition of old spurs or barren spurs be made to approach that of young vigorous bearing spurs and thus the spur be made productive?

Certain trees and certain varieties are alternate bearers, while other trees or varieties are regular bearers. Is it because of differences in the absorption or utilization of certain food materials in the spring, or perhaps because of differences in the storage of food materials during the summer and fall?

In what way and to what extent can the chemical equilibrium within the plant be modified by treatments such as tillage, fertilization and pruning? May not correlations exist which will make it possible to modify one factor, indirectly thru the control of some other? This might open a way for the regulation of important factors that could not be influenced by direct orchard treatment. Thus, for example, may not such a significant factor as the starch content be modified indirectly by altering the nitrogen or phosphorus content at some crucial period?

Many other questions present themselves. The answers to some may be negative, to others of doubtful importance. In any case the investigation upon which this is a first report will, it is hoped, afford a better understanding of what is taking place within the tree and may eventually lead to a more thoro knowledge of the effects of certain cultural practices on growth and production.

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APPENDIX

The figures given in the following tables are averages of duplicate analyses. In the few cases where it was necessary analyses were repeated until duplicates were obtained which checked within the limits given in the following table. In order to give a conception of the accuracy of the determinations, the average deviation is indicated, in addition.

	Limits of deviation allowed	Average deviation	Approximate total
Ash	0.6 %	0.15 %	in 7 %
Acidity	0.2 cc.	0.1 cc.	in 2 cc
Potassium	0.05 %	0.02 %	in 0.5 %
Phosphorus	0.04 %	0.01 %	in 0.2 %
Nitrogen	0.2 %	0.05 %	in 1 %
Sugars and starch	0.4 %	0.1 %	in 2 %
Total polysaccharides	2 %	0.5 %	in 25 %

TABLE 1.—DRY WEIGHT IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	50.1	34.5	38.9	46.8	49.5	54.3
Ben Davis.....	40.0	35.4	38.2	44.8	48.4	48.9	
Jonathan	52.5	36.8	39.8	45.2	48.4	52.3	
<i>Non-Bearing Spurs</i>								
Jonathan	52.9	45.2	47.0	48.6	51.4	50.4	
Ben Davis.....	49.2	40.2	44.9	51.4	51.5	51.1	
<i>Barren Spurs</i>								
Ben Davis	54.4	47.3	52.2	52.4	55.4	54.5	
Nixonite	52.6	43.8	48.6	52.4	51.4	56.9	

TABLE 2.—ASH IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	11.02	8.72	7.075	9.610	8.16	9.11
Ben Davis.....	8.44	8.44	5.408	4.560	5.39	7.47	
Jonathan	7.38	7.92	6.115	5.663	6.11	7.00	
<i>Non-Bearing Spurs</i>								
Jonathan	6.92	6.86	6.668	7.353	7.50	9.31	
Ben Davis.....	5.24	4.96	4.873	5.765	6.73	8.42	
<i>Barren Spurs</i>								
Ben Davis	8.01	7.31	7.425	8.603	7.50	9.08	
Nixonite	10.37	8.55	7.743	9.700	9.22	10.23	

TABLE 3.—ASH IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 11	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	5.52	3.01	2.76	4.50	4.04	4.94
Ben Davis.....	3.38	2.99	2.07	2.04	2.61	3.66
Jonathan	3.88	2.92	2.44	2.56	2.96	3.66
<i>Non-Bearing Spurs</i>								
Jonathan	3.66	3.10	3.14	3.57	3.86	4.69
Ben Davis.....	2.58	1.99	2.19	2.97	3.47	4.30
<i>Barren Spurs</i>								
Ben Davis.....	4.41	3.46	3.88	4.51	4.16	4.95
Nixonite	5.46	3.75	3.76	5.08	4.65	5.82

TABLE 4.—TITRATABLE ACIDITY IN CC. OF N/10 ACID PER GRAM OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	2.04	2.58	3.40	1.74	1.92	2.42
Ben Davis.....	1.96	2.50	2.98	2.22	1.76	2.60
Jonathan	1.30	2.96	3.51	1.82	1.60	2.28
<i>Non-Bearing Spurs</i>								
Jonathan	1.54	2.64	2.14	1.78	1.80	2.24
Ben Davis.....	1.70	2.50	2.06	1.90	1.56	2.04
<i>Barren Spurs</i>								
Ben Davis.....	1.72	2.80	1.70	1.40	1.16	2.10
Nixonite	1.84	2.37	1.81	1.50	1.40	1.86

TABLE 5.—TITRATABLE ACIDITY IN CC. OF N/10 ACID PER GRAM FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	1.02	0.89	1.32	0.81	0.95	1.32
Ben Davis.....	0.78	0.89	1.14	0.99	0.85	1.27
Jonathan	0.68	1.09	1.40	0.82	0.93	1.19
<i>Non-Bearing Spurs</i>								
Jonathan	0.81	1.20	1.01	0.87	0.93	1.13
Ben Davis.....	0.84	1.01	0.93	0.87	0.80	1.04
<i>Barren Spurs</i>								
Ben Davis.....	0.94	1.33	0.89	0.73	0.64	1.15
Nixonite	0.97	1.04	0.88	0.79	0.72	1.06

TABLE 6.—POTASSIUM IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.610	1.01	0.81	0.689	0.805	0.740
Ben Davis.....	0.709	0.98	0.72	0.465	0.572	0.547
Jonathan	0.583	1.05	0.88	0.581	0.682	0.590
<i>Non-Bearing Spurs</i>								
Jonathan	0.583	0.63	0.72	0.488	0.571	0.576
Ben Davis.....	0.547	0.68	0.66	0.571	0.539	0.594
<i>Barren Spurs</i>								
Ben Davis.....	0.487	0.54	0.46	0.405	0.416	0.524
Nixonite	0.553	0.58	0.51	0.452	0.572	0.551

TABLE 7.—POTASSIUM IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.306	0.348	0.315	0.325	0.398	0.402
Ben Davis.....	0.284	0.347	0.275	0.208	0.278	0.267
Jonathan	0.306	0.386	0.351	0.263	0.330	0.309
<i>Non-Bearing Spurs</i>								
Jonathan	0.308	0.285	0.338	0.237	0.294	0.390
Ben Davis.....	0.269	0.273	0.296	0.293	0.278	0.304
<i>Barren Spurs</i>								
Ben Davis.....	0.265	0.256	0.240	0.212	0.230	0.286
Nixonite	0.291	0.254	0.248	0.237	0.294	0.314

TABLE 8.—PHOSPHORUS IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.241	0.272	0.229	0.203	0.199	0.264
Ben Davis.....	0.272	0.252	0.213	0.195	0.195	0.225
Jonathan	0.237	0.339	0.246	0.192	0.211	0.255
<i>Non-Bearing Spurs</i>								
Jonathan	0.203	0.116	0.262	0.190	0.223	0.280
Ben Davis.....	0.240	0.156	0.176	0.158	0.195	0.234
<i>Barren Spurs</i>								
Ben Davis.....	0.166	0.105	0.146	0.149	0.157	0.183
Nixonite	0.240	0.152	0.216	0.163	0.192	0.240

TABLE 9.—PHOSPHORUS IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.121	0.094	0.089	0.095	0.099	0.142
Ben Davis.....	0.109	0.089	0.081	0.087	0.094	0.110
Jonathan	0.125	0.125	0.098	0.087	0.102	0.133
<i>Non-Bearing Spurs</i>								
Jonathan	0.107	0.052	0.123	0.092	0.115	0.141
Ben Davis.....	0.118	0.063	0.079	0.081	0.101	0.120
<i>Barren Spurs</i>								
Ben Davis.....	0.090	0.050	0.076	0.078	0.087	0.100
Nixonite	0.126	0.067	0.105	0.085	0.099	0.137

TABLE 10.—TOTAL NITROGEN IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	1.30	1.84	1.108	1.022	1.000	1.088
Ben Davis.....	1.45	1.83	1.156	1.114	1.017	1.191
Jonathan	1.14	1.61	0.974	1.022	0.916	1.083
<i>Non-Bearing Spurs</i>								
Jonathan	1.03	0.87	0.802	0.968	1.017	1.192
Ben Davis.....	1.31	1.01	0.620	0.813	0.983	1.181
<i>Barren Spurs</i>								
Ben Davis.....	1.13	0.78	0.658	0.822	0.836	0.855
Nixonite	0.98	0.83	0.687	0.777	0.811	0.851

TABLE 11.—TOTAL NITROGEN IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.652	0.634	0.431	0.478	0.495	0.590
Ben Davis.....	0.580	0.648	0.443	0.499	0.492	0.582
Jonathan	0.598	0.592	0.388	0.462	0.443	0.565
<i>Non-Bearing Spurs</i>								
Jonathan	0.545	0.393	0.377	0.471	0.523	0.601
Ben Davis.....	0.644	0.406	0.279	0.418	0.506	0.604
<i>Barren Spurs</i>								
Ben Davis.....	0.615	0.369	0.350	0.431	0.513	0.466
Nixonite	0.515	0.364	0.334	0.407	0.417	0.484

TABLE 12.—REDUCING SUGARS AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	3.74	0.30	1.19	1.24	2.16	4.84
Ben Davis.....	1.42	0.23	1.87	2.14	2.48	4.53
Jonathan	3.63	0.38	1.69	1.76	2.63	4.22
<i>Non-Bearing Spurs</i>								
Jonathan	3.63	1.17	1.35	1.31	2.36	4.00
Ben Davis.....	2.09	0.65	1.04	1.22	1.69	3.06
<i>Barren Spurs</i>								
Ben Davis.....	1.43	0.84	0.66	0.97	1.87	3.13
Nixonite	2.45	1.37	0.61	1.28	1.62	2.53

TABLE 13.—REDUCING SUGARS AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	1.88	0.10	0.463	0.580	1.07	2.58
Ben Davis.....	0.568	0.08	0.715	0.960	1.20	2.26
Jonathan	1.91	0.14	0.673	0.795	1.27	2.21
<i>Non-Bearing Spurs</i>								
Jonathan	1.92	0.53	0.635	0.636	1.21	2.02
Ben Davis.....	1.030	0.26	0.467	0.627	0.87	1.56
<i>Barren Spurs</i>								
Ben Davis.....	0.778	0.40	0.345	0.508	1.04	1.71
Nixonite	1.29	0.60	0.297	0.670	0.83	1.44

TABLE 14.—NON-REDUCING SUGARS AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	0.66	0.33	0.00	0.29	1.84	0.16
Ben Davis.....	0.59	0.24	0.00	0.00	0.64	0.93
Jonathan	0.49	0.73	0.00	0.00	1.33	0.57
<i>Non-Bearing Spurs</i>								
Jonathan	0.25	0.00	0.00	0.49	0.49	3.09
Ben Davis.....	0.68	0.53	0.10	0.40	1.04	1.69
<i>Barren Spurs</i>								
Ben Davis.....	1.30	0.26	0.00	0.71	1.37	1.41
Nixonite	0.64	0.63	0.38	0.01	1.11	2.24

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TABLE 15.—TOTAL SUGARS AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	4.40	0.63	1.19	1.53	4.00	5.00
Ben Davis.....	2.01	0.47	1.87	2.14	3.12	5.45
Jonathan	4.12	1.01	1.69	1.76	3.96	4.79
<i>Non-Bearing Spurs</i>								
Jonathan	3.78	1.17	1.35	1.80	2.85	7.09
Ben Davis.....	2.77	1.18	1.14	1.62	2.73	4.75
<i>Barren Spurs</i>								
Ben Davis.....	2.73	1.10	0.66	1.68	3.24	4.54
Nixonite	3.09	2.00	0.99	1.29	2.73	4.77

TABLE 16.—TOTAL SUGARS AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	2.21	0.22	0.46	0.72	1.98	2.72
Ben Davis.....	0.80	0.17	0.71	0.96	1.51	2.67
Jonathan	2.16	0.37	0.67	0.79	1.92	2.50
<i>Non-Bearing Spurs</i>								
Jonathan	2.00	0.53	0.63	0.88	1.47	3.57
Ben Davis.....	1.36	0.47	0.51	0.83	1.41	2.43
<i>Barren Spurs</i>								
Ben Davis.....	1.49	0.52	0.34	0.88	1.81	2.48
Nixonite	1.63	0.88	0.48	0.68	1.40	2.71

TABLE 17.—STARCH AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	4.81	Trace	Trace	5.63	2.57	1.35
Ben Davis.....	4.75	Trace	Trace	4.20	1.98	1.51
Jonathan	4.53	Trace	Trace	3.00	1.55	1.82
<i>Non-Bearing Spurs</i>								
Jonathan	2.18	Trace	2.16	4.20	2.38	2.16
Ben Davis.....	5.05	Trace	3.16	4.85	2.12	2.05
<i>Barren Spurs</i>								
Ben Davis.....	0.99	Trace	Trace	1.72	1.67	0.86
Nixonite	1.24	Trace	Trace	2.81	1.82	1.53

TABLE 18.—STARCH AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	2.41	Trace	Trace	2.64	1.27	0.73
Ben Davis.....	1.90	Trace	Trace	1.88	0.98	0.74
Jonathan	2.38	Trace	Trace	1.36	0.75	0.96
<i>Non-Bearing Spurs</i>								
Jonathan	1.15	Trace	1.02	2.04	1.22	1.09
Ben Davis.....	2.49	Trace	1.42	2.49	1.09	1.06
<i>Barren Spurs</i>								
Ben Davis.....	0.54	Trace	Trace	0.90	0.93	0.47
Nixonite	0.65	Trace	Trace	1.47	0.94	0.87

TABLE 19.—TOTAL POLYSACCHARIDES MINUS STARCH AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	11.81	19.06	25.80	32.87	21.81	18.33
Ben Davis.....	14.13	19.70	22.62	22.60	24.77	17.74	
Jonathan	15.47	19.87	20.89	31.60	20.81	17.86	
<i>Non-Bearing Spurs</i>								
Jonathan	17.45	20.57	18.96	22.43	19.84	15.09	
Ben Davis.....	19.06	25.05	23.72	25.28	18.98	16.70	
<i>Barren Spurs</i>								
Ben Davis.....	19.90	23.75	21.93	23.73	17.58	18.51	
Nixonite	14.88	18.78	25.00	22.39	20.43	18.72	

TABLE 20.—POLYSACCHARIDES MINUS STARCH AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	5.91	6.58	10.04	15.39	10.80	9.95
Ben Davis.....	5.66	6.97	8.65	10.13	11.97	8.67	
Jonathan	8.12	7.31	8.32	14.29	10.08	9.32	
<i>Non-Bearing Spurs</i>								
Jonathan	9.22	9.29	8.91	10.91	10.21	7.60	
Ben Davis.....	9.38	10.80	10.66	13.00	9.79	8.52	
<i>Barren Spurs</i>								
Ben Davis.....	10.83	11.23	11.45	12.44	9.74	10.09	
Nixonite	7.82	8.22	12.15	11.73	10.50	10.65	

TABLE 21.—TOTAL POLYSACCHARIDES AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	16.62	19.06	25.80	38.50	24.38	19.68
Ben Davis.....	18.88	19.70	22.62	26.80	26.75	19.25	
Jonathan	20.00	19.87	20.89	34.60	22.36	19.68	
<i>Non-Bearing Spurs</i>								
Jonathan	19.63	20.57	21.12	26.63	22.22	17.25	
Ben Davis.....	24.12	25.05	26.88	30.12	21.10	18.75	
<i>Barren Spurs</i>								
Ben Davis.....	20.89	23.75	21.93	25.45	19.25	19.37	
Nixonite	16.12	18.78	25.00	25.20	22.25	20.25	

TABLE 22.—TOTAL POLYSACCHARIDES AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	8.32	6.57	10.04	18.03	12.07	10.68
Ben Davis.....	7.56	6.97	8.65	12.01	12.95	9.41	
Jonathan	10.50	7.31	8.32	15.65	10.83	10.28	
<i>Non-Bearing Spurs</i>								
Jonathan	10.40	9.29	9.93	12.95	11.43	8.69	
Ben Davis.....	11.89	10.08	12.08	15.49	10.88	9.58	
<i>Barren Spurs</i>								
Ben Davis.....	11.37	11.23	11.45	13.34	10.67	10.56	
Nixonite	8.48	8.22	12.15	13.20	11.44	11.52	

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TABLE 23.—TOTAL CARBOHYDRATES AS GLUCOSE IN PERCENTAGES OF DRY WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	21.02	19.69	26.99	40.03	28.38	24.68
Ben Davis.....	20.89	20.17	24.49	28.94	29.87	24.71	
Jonathan	24.12	20.88	22.58	36.36	26.32	24.47	
<i>Non-Bearing Spurs</i>								
Jonathan	23.41	21.74	22.47	28.43	25.07	24.34	
Ben Davis.....	26.89	26.23	28.02	31.75	23.83	23.50	
<i>Barren Spurs</i>								
Ben Davis.....	23.62	24.85	22.59	27.13	22.49	23.91	
Nixonite	19.21	20.78	25.99	26.49	24.98	25.02	

TABLE 24.—TOTAL CARBOHYDRATES AS GLUCOSE IN PERCENTAGES OF FRESH WEIGHT

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	10.53	6.79	10.50	18.75	14.05	13.40
Ben Davis.....	8.36	7.14	9.36	12.97	14.46	12.09	
Jonathan	12.66	7.68	8.99	16.44	12.75	12.88	
<i>Non-Bearing Spurs</i>								
Jonathan	12.40	9.82	10.56	13.83	12.90	12.26	
Ben Davis.....	13.23	10.55	12.59	16.32	12.29	12.01	
<i>Barren Spurs</i>								
Ben Davis.....	12.86	11.75	11.79	14.22	12.48	13.04	
Nixonite	10.11	9.10	12.63	13.88	12.84	14.23	

TABLE 25.—HYDROGEN ION CONCENTRATION AS pH

	Feb. 4	Mar. 11	Mar. 26	May 13	June 26	Sept. 2	Nov. 19	Jan. 24
<i>Bearing Spurs</i>								
Wealthy	5.8	5.6	5.7	5.9	6.0	5.9
Ben Davis.....	5.6	5.4	5.5	5.7	5.6	5.5	
Jonathan	5.6	5.5	5.7	5.7	5.8	5.6	
<i>Non-Bearing Spurs</i>								
Jonathan	5.7	5.8	5.9	5.9	5.9	5.8	5.8
Ben Davis.....	5.4	5.5	5.6	5.9	5.6	5.5	
<i>Barren Spurs</i>								
Ben Davis.....	5.5	5.4	5.6	5.9	5.7	5.6	
Nixonite	5.8	5.8	5.9	5.9	5.5	5.5	

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